PRACTICAL PLANT ECOLOGY

A GUIDE FOR BEGINNERS IN FIELD STUDY OF PLANT COMMUNITIES

BY

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PREFACE

THIS book is intended as a guide for those who are attracted to ecological work, but are uncertain as to how to set about it.

Parts I and II aim at providing the minimum theoretical basis which will serve as a satisfactory framework for field studies of plant communities. The chief climax units of vegetation—association, consociation and society—are adopted from Clements's scheme.[1] They seem to the author the most satisfactory working units, and they have been taken up and successfully used by several of the best recent British workers. The conception of a climax is not, however, restricted to the climatic climax, but is applied to any relatively stable and well characterised community determined by any actual combination of persistent factors, including biotic factors.[2] The seral units are explained in a footnote on page 47, and may be used by anyone who is working at succession and who finds them useful. The conception of a plant formation has been wholly omitted, in view of the different senses in which it is employed by Continental European workers on the one hand, and the English and Americans on the other. It is not an essential conception for the purposes of the present work, in which theoretical discussion is intentionally reduced to a minimum.

Part III deals with the study of vegetation itself. The necessity of definite aims is first insisted upon, and some indication of what these aims should be is given. The different methods of studying vegetation by means of the making of maps and charts are described, with insistence on the danger of turning methods into ends—the true end

[1] F. E. Clements, *Plant Succession* (Carnegie Institution of Washington, 1916). See *Journal of Ecology*, **4**. p. 199, 1916.

[2] Readers who are interested in the theory of plant communities are referred to my theoretical discussion in "The Classification of Vegetation and the Concept of Development." *Journal of Ecology*, **8**. p. 118, 1920.

of all work on vegetation being the knowledge and unde standing of it.

Part IV deals with habitat analysis in an elementa: manner, methods demanding much special training bei omitted. At the risk of appearing content with superfici work on the habitat, I have preferred to endeavour concentrate attention on the vegetation itself, being co vinced that such concentration is not only more fruitf for the beginner, but is more likely than too highly specialis habitat work to lead to sound advance in our knowled of vegetation. We sometimes tend to forget the plan and their struggles for the sake of the measurement of sing habitat factors, of which we may easily exaggerate t importance. This is not, of course, to suggest that beginne should ignore the habitat altogether, nor that advanc workers should fail to push the analysis of factors and the combinations to the furthest possible point. On the oth hand, there are few of us who would not be the wiser f paying more attention than we commonly do to the behavio and relations of the plants themselves.

Part V deals with school-work in ecology, for which the may be a great future if interest and enthusiasm can aroused in adequate measure. The "nature study" nc very widely pursued in the lower forms of schools is suggest as the proper foundation for ecological work, and a pl is put forward for the development of this on ecologic lines, *in schools where the opportunities are good,* througho the school course. It is not for a moment supposed that a school could adopt the whole of the suggestions contain in Part V. But it is hoped that among these there m be found material which will be useful for practical develo ment as outdoor work, sometimes perhaps as part of a cour in practical geography, sometimes for the widening, if n the foundation, of a laboratory or classroom course botany. Probably all serious and systematic outdoor wo is more trouble to the teacher than indoor work, but it

believed that the extra labour will be fully repaid by the interest aroused.

The Appendix contains additional information on various topics, which could not be treated more fully in the text without overloading the various chapters.

Finally, there is a fairly full list of papers on British vegetation, arranged geographically, so that would-be students of vegetation in different parts of the country may learn what has been done in their neighbourhood on modern lines. It is unfortunate that many of the older papers are comparatively inaccessible, but during the last decade most of the British work has been published in *The Journal of Ecology*, which is readily obtainable. It may be mentioned here that this journal is published by the Cambridge University Press at 20s. for the annual volume, and that all the back numbers are available. Membership of the British Ecological Society (Secretary, Dr. E. J. Salisbury, The Briars, Crosspath, Radlett, Herts), which owns the *Journal of Ecology*, is open to all. The annual subscription is 25s., which includes, of course, the right to attend the meetings at which papers are read and discussed, and the summer excursions, as well as free delivery of the *Journal* and other privileges.

There are, so far as my knowledge goes, only two books in existence which have at all the same objects as this—Dr. Clements's *Research Methods in Ecology* (1905) and Dr. Rübel's *Geobotanische Untersuchungsmethoden* (1922). Both are admirable and most useful works, but neither is suitable for the British student who has little previous knowledge of the subject. In thus attempting to meet what I believe is a widespread need, I was confronted with many difficulties, mainly concerned with what should be included in and what should be omitted from a book whose length it was desirable to restrict so that it could be issued at a reasonable price. I therefore sought to supplement

my own judgment with that of other British ecologists, and two ex-presidents of the British Ecological Society—Dr. W. G. Smith and Professor R. H. Yapp—as well as that admirable critic, Mr. S. M. Wadham, Senior Demonstrator in Botany at Cambridge, have had the great kindness to read the manuscript and criticise it in detail. I owe the most cordial thanks to these three gentlemen, all of whose suggestions have been most valuable, very nearly all having been adopted. While I cannot involve my helpful critics in responsibility for the contents and treatment, I was greatly encouraged to find that they all felt the book was on the right lines and would meet a real want.

I have also most gratefully to thank Dr. H. J. Page, of the Rothamsted Experimental Station, for very kindly contributing the section of the Appendix on the determination of carbonates and bases in soil; and Mr. Hamshaw Thomas for writing some paragraphs on the photography of vegetation.

The author will welcome criticisms and suggestions for improvement in view of a second edition.

British ecology was hard hit by the war. In 1914 it was just entering on a new phase of development which promised to be exceedingly fruitful. The war killed some of the ablest and most enthusiastic of the younger workers and broke up several promising schemes of work. International co-operation was suspended, and even yet cannot be fully resumed. All things considered, progress during the last decade has been greater than could be expected. But in view of the serious obstacles to ecological work that still exist at our universities it is more than ever necessary to enroll recruits from the schools and from among private students of nature. It is hoped that the present effort to provide a practical guide to work in the field may not be without effect in the desired direction.

A. G. T.

GRANTCHESTER, CAMBRIDGE,
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INTRODUCTORY

CHAPTER I

WHAT IS ECOLOGY?

THE word ECOLOGY, as is well known, is derived, like the common word *economy*, from the Greek *οἶκος* (oikos), *house, abode, dwelling*. In its widest meaning ecology is the study of plants and animals *as they exist in their natural homes*; or better, perhaps, the study of their *household affairs*, which is actually a secondary meaning of the Greek word.

In this book we shall confine ourselves to plant ecology. For various reasons it is more developed and more readily accessible to the beginner than animal ecology. The latter is often not easily attacked without some considerable knowledge of the vegetation, because very many animals depend directly upon plants for shelter, while all depend upon them, directly or indirectly, for food. Plants form the basis of all life as it is lived upon the earth, because they alone have the power of making organic substance from inorganic, of building up living substance from materials like carbon dioxide, water and mineral salts. Animals can only use the results of this work of plants, either by directly eating them (herbivorous animals), or by eating other animals which have fed upon plants. In a favourable climate and soil plants cover the ground more or less completely, thus *forming a natural framework or basis for the study of the living populations of the globe*. In this way they determine not only the food but largely also the shelter

and general conditions of life of the animal and human communities.

In its widest sense ecology must cover the study of the "household affairs" of animals, including man, not only because animals form an important part of the life existing on the surface of the earth, but because the effects of animals upon plants are numerous and far-reaching; while man, of course, occupies a unique position owing to his far-extended control over nature. Thus anything like a *complete* study of the ecology of a plant community necessarily includes a study of the animals living in or feeding upon it. The influence of man upon plant communities is of first importance in all but the uninhabited and the most sparsely inhabited regions of the earth. As we shall see in later chapters, we can never afford to lose sight of past and present human activities in their effects on the vegetation of countries which have been long inhabited and densely populated, like those of Western and Central Europe. But though we must thus constantly take account of the effects of animals upon plants, we shall here be concerned entirely with plant ecology —our centre of interest will be the plants themselves.

It is clear that in the wide sense defined above, plant ecology cannot properly be considered a *separate branch* of botany, since it must include a great number of topics which certainly belong to the older well-recognised divisions of our knowledge of plants. Thus, if we are going to study the household affairs of plants as they grow in nature, we must first of all learn to distinguish the different kinds or species of plants with which we have to deal, and for this purpose we must have some knowledge of *taxonomy*, or, as it is often called, *floristic botany*. Then we must understand the *construction* of the plant body, the differences between its different members, how they grow from the seed or from one another—and this is a part of *morphology* or *organography*. Further, we must know something of the *minute anatomy* or *histology* of plants if we desire to penetrate at all

deeply into the reactions of plants to the different environments in which they grow. Again, we must study how far plants depend on insects or the wind for fertilisation, or how far they fertilise themselves, the ways in which they spread from place to place, the means by which they propagate themselves and are dispersed (fruits, seeds, rhizomes, runners, etc.). All these last-mentioned topics used to be included under the name "biology," or "bionomics" of plants, but the former name should be restricted to the science of life as a whole, and the latter is more frequently used by zoologists. Finally, every attempt to ascertain the actual causes that underlie the ability of some kinds of plants to flourish in particular situations, while others cannot, will certainly lead, not only to questions of the means of dispersal already mentioned, and of the influence of animals and of human activity, but also to a study of soil and climate in their relation to different species. This last investigation leads directly to a study of the physical and chemical relations of the plant and its habitat, involving some of the most difficult problems of plant *physiology*, problems which occupy the attention of many of the ablest specialists.

Thus it becomes clear that plant ecology in the wide sense is more A MEANS OF APPROACH TO A LARGE PART OF DETAILED BOTANICAL STUDY than a name for a special branch of the subject, such, for instance, as histology (the study of tissues), cytology (the study of cells), or, again, the study of a particular group of plants like the mosses or the fungi. It is important to emphasise this fact because the modern popularity of ecology depends largely upon it. This popularity represents a reaction from the kind of botany which dealt only with plants in narrowly defined aspects, such as the study of anatomy, of physiology, and of the different groups of the plant kingdom. That sort of study is most conveniently pursued in laboratories to which the plants to be studied are brought, and much of it can only be carried out with the aid of laboratory equipment. The result of

its too exclusive pursuit is to remove the student altogether from plants as they actually live in their homes; and in the absence of continual contact with these his knowledge becomes curiously limited and one-sided, though it may be profound within its limits. Occasional field excursions do not suffice to correct this tendency, for even when taken seriously they are almost always limited to collecting and naming the species met with—there is rarely time for anything more. *Ecology must be studied primarily in the field,* though it is often desirable or necessary to continue in the laboratory the investigation of special points which cannot be decided without books, microscopes, or laboratory apparatus.

A parallel may be found in the study of man. The human anatomist and the human physiologist have, each in his own sphere, a profound knowledge of man, and the two together can give a fairly complete general account of the structure and working of the human body. But no one would contend that such knowledge covers the field of what we may know about man and his activities. It is not sufficient to study the structure of his dead body in the dissecting room, or the functions of his organs and tissues in the physiological laboratory. To learn what man actually is and does in the world, we have to go out into the world and study him as he lives and works among his fellows. And the same is true of plants.

Plants are gregarious beings, because they are mostly fixed in the soil and propagate themselves largely in social masses, either from broadcast seed (or spores), or vegetatively by means of rhizomes, runners, corms, or bulbs, sometimes by new shoots ("suckers") arising from the roots. In this way they produce *vegetation,* as plant growth in the mass is conveniently called, and this is found to fall naturally into *plant communities,* or *units of vegetation.* Now, these plant communities have structures, activities and laws of their own. Each has an internal economy depending on the relations of its individual members to one another:

also an origin, history, and fate. Particular communities can exist in some places and not in others, depending on the conditions of soil and climate and on their relations to other plant communities and to animals. Within the larger communities smaller ones exist. In these features we recognise parallels with the nations, tribes, and societies of mankind, though the members of plant communities are not so closely knit as the members of human, and even of the higher animal, communities, by a complex physical and psychical interdependence. Plant communities are also essentially different from human communities, in that they are commonly composed not of a single species of organism, but of several or many different species living together.

The main causes of the specific structure and individuality of a given plant community are: first, the fact that only those species can be present in it which exist in the particular part of the world, and which are able to reach the particular spot; secondly, that only those can be present which are able to exist under the given conditions of life, and in competition with the other species present; and thirdly, that in many communities certain species can only survive in the presence of others, for instance the shade plants of a forest floor under the trees which cast the shade.

The systematic study of plant communities is on the whole a modern study, though types of vegetation and their dependence on conditions of life have been recognised for a long time. The active modern study of these types is, however, not much more than a quarter of a century old. In Great Britain especially "ecology" has tended to become identified with the study of plant communities, because both the general use of the name and the organised study of communities were largely determined by the publication in 1896 of the German edition, entitled *Ecological Plant Geography*, of the pioneer work by Professor Warming of Copenhagen. This identification is not, however, justified. As we have seen, ecology in the wide sense is much broader.

Synecology, from the Greek *σύν*, *together*, is often used for the study of communities, as distinct from *autecology* (Greek *αὐτός*, *self*, *by oneself*, *alone*), or the study of the ecology of individual species. Modern Continental workers, and they are being followed by some American authors, are tending more and more to use the term *plant sociology* for the study of plant communities as such. They confine the word *ecology* to the study of the *habitat*, the *oikos* itself, of a plant or of a community, i.e. of the sum total of the effective conditions which determine the existence of the plant or community in a given spot. This is certainly a strictly logical use. Nevertheless, in this book the word is employed in the wider meaning at first described, for it is important, especially in a book intended for beginners, to keep the emphasis on ecology as the approach to botany through the direct study of plants in their natural conditions. In this approach a knowledge of plant communities, their structure, economy, origin and fate (plant sociology) must bulk very largely.

Ecology in this wide sense is of the greatest importance in schools, because from the outset it introduces the pupil to plants as they actually exist, and to the parts they play in the world, and avoids the narrow one-sided ways of looking at plants that the older-fashioned methods of teaching botany, if pursued alone, tend to develop.

CHAPTER II

NATURAL AND SEMI-NATURAL VEGETATION

By natural vegetation we mean of course vegetation primarily due to "nature" rather than to man. To take extreme cases: a virgin forest is clearly natural, while a wheat or "root" crop is clearly not. But we have to recognise at once that there are a great many cases intermediate between these two extremes. If we leave out of account all the genuinely virgin untouched communities on the one side, and all sown field crops and plantations on the other, we find that large parts of the vegetation of a country like Great Britain, more especially of the north and west, but considerable tracts also in the south and east, owe their character partly to nature and partly to human activity. If the vegetation itself is spontaneous, i.e. has occupied the ground without the aid of direct human action, but has nevertheless been partly determined or markedly modified by man or his animals, we class it as "semi-natural."

Thus natural woods which are "selectively" felled (i.e. from which single trees are periodically taken out), but not "clear felled" and replanted, and those which are regularly coppiced; heaths and moors, which are periodically burned or regularly pastured; grassland which has not been sown, but which is regularly pastured or mowed; marshes which are drained and pastured, or periodically cut, are semi-natural vegetation. The great bulk of the forest and "waste land" of the British Isles is in this condition. True "virgin" communities of any size are rare, indeed practically absent, except on the seacoast and in the remoter mountain regions. But there are a good many which are substantially natural,

having been interfered with only by occasional felling, pasturing, or burning, and many more which are semi-natural, i.e. they represent a definite modification of a natural community, and are kept in their existing condition only by the activity of man.

The degree to which man has influenced an apparently natural community varies, of course, very considerably, and has often to be made the subject of special investigation. Continued selective felling of the trees in a natural wood, the constant cutting out of certain kinds only, will, for instance, gradually alter the proportional composition of the wood, and sometimes its whole character. Again, the opening of the wood canopy and the consequent letting in of light will kill certain woodland plants and promote the growth of others. It will also allow the entrance of herbs and grasses which could not grow at all in the deep shade, and these will tend to suppress those true shade plants of the woodland floor which have survived, and to compete with the species whose growth has been stimulated, so that the constitution of the ground vegetation may be entirely altered. Pasturing and burning of grassland or heath will destroy some species and severely check the development of others, while certain species will shoot again quickly after being eaten down or burned, thus altering the composition of the herbage. Others, again, which could not find a footing in the original plant community, will invade burned or very heavily pastured land, because they find there open or sparsely covered spots which would not exist apart from the burning or overgrazing. Lowering the water level of a marsh or fen, or of low-lying alluvial land, by drainage, will kill out certain species and weaken others, while it will admit fresh colonists that flourish in a drier soil. All these effects, and others of a similar nature, have constantly to be taken into account in studying semi-natural vegetation.

A belief is sometimes met with that only perfectly "natural" vegetation is a proper subject for ecological study. If this were true, the ecological field in Great Britain

would be very limited indeed. Fortunately, the belief is entirely mistaken. The laws governing the behaviour of plants, their relations to one another, and their formation of communities, are the same whether the activity of man and his domestic animals plays a part or not. It is true that ecological problems are complicated by man's activity —fresh factors have to be considered. But the plants themselves are working in the same way, tending towards the same effects, whether man is at work or not. The only practical difference is that the plant communities and their distribution (apart altogether from actually cultivated areas) are to a considerable extent different in countries where most of the land has long been subject to human interference from those still untouched or only slightly touched by human agency.

In the countries which have long been the seats of civilisation it is not always a simple matter to reconstruct the "original" vegetation. But this can usually be done with a fair degree of certainty when sufficient detailed knowledge of the behaviour of the native plants and the communities they form has been obtained and a comparison made with neighbouring countries having a similar climate and flora, but perhaps with different methods of forestry and agriculture. On the other hand, man is always unwittingly performing ecological experiments on a small or a large scale, experiments which the ecologist can watch and the results of which he can trace out and record, thus slowly gaining an extensive knowledge of the capacities of plants, of their reactions to changed conditions, which the observer in a "virgin country" cannot easily acquire.

It is true that the farmer, landowner, or "local authority" sometimes carries his experiments further than the ecologist would desire. The observation of a process of recolonisation of a piece of cleared land, for instance, may be rudely interrupted by digging for gravel, road-making, or building. Interesting and instructive bits of vegetation are often destroyed by some fresh outburst of energy on the part of

"higher powers," all the more irritating when it is clearly not wisely directed. But the observer who can put up with such disappointments, and who will never lose an opportunity of observing and comparing what is going on, can learn a great deal if he will adapt himself to the conditions of the country-side in which he lives.

Even the most highly cultivated parts of the country, where the land is almost all under the plough, offer numerous opportunities for ecological study. Such are great tracts of the Eastern Counties of England, considerable parts of the Southern Counties, parts of the Midlands, the south Lancashire and Cheshire plains, etc. First of all there are the roadsides and hedge banks, which bear semi-natural plant communities—the former often very similar to those of pastureland or on barren sands of heathland, the latter consisting mainly of "marginal" woodland species, i.e. those which grow on the edges of woods under similar conditions of soil and climate. These both provide good subjects for study and comparison. Secondly, there are the weeds of the arable land itself, which differ according to climate, soil and crop rotation. And finally there are the crops themselves, which are by no means the least interesting communities, though they are entirely artificial. Scientific agriculture, indeed, is largely applied ecology. The field crops which *can be* successfully cultivated on a given piece of land depend, of course, on the climate and soil, just as does the natural vegetation; but the crops which actually *are* cultivated depend also upon the existence and accessibility of markets, so far as they are not used locally.

The grass fields of "permanent pasture" which occupy so much of the Midlands and West of England are really semi-natural plant communities, for though they may in many cases have been "laid down to pasture" by sowing ploughed land with grass, they quickly become modified by the natural immigration of herbs and grasses, so that sometimes few of the kinds of grass sown ultimately remain. The composition of the flora of permanent pasture varies

with the soil, the water supply, the proximity of neighbouring natural vegetation, and also with the kind and amount of pasturing and manuring.

Tree plantations on arable land (which are not common), and on grassland or old cleared woodland (the usual sites for planting), may become the equivalents of semi-natural plant communities, though the trees have been actually planted. This is the case when the trees planted are of the species that form natural woods on the same soil. Woodland plants gradually colonise the plantation, and in course of time it becomes practically indistinguishable from a natural wood (**55** Woodruffe-Peacock, 1918). This process occurs much more quickly if the plantation is made on old cleared woodland, because the old humus and some of the old woodland plants remain, so that the process of approximation to the condition of a natural wood is accelerated. If unsuitable trees are planted along with suitable ones, the former die out, either as the direct effect of the unsuitable soil, or as the result of overshadowing by the kinds which are at home, or from both these causes, just as unsuitable grasses disappear from sown pasture.

Plantations of exotic trees, particularly conifers—spruce, pine and larch are the kinds most commonly planted in this country—provide examples of artificial communities, differing, as regards the ground vegetation, more or less considerably from our natural woods. Sometimes they are invaded by "weeds," sometimes certain woodland plants obtain a footing in the plantation, sometimes the soil remains or becomes practically bare. In any case the plantation affords some opportunity for ecological observation and comparison, even where the results are chiefly negative.

Thus there is plenty of work for the ecologist in highly cultivated districts, though it is not quite of the same kind as in regions which are mainly occupied by natural or semi-natural vegetation. Even building sites and roads, which have been laid out and left derelict for a time, and similar places, often present the material for interesting study.

Such habitats are not of course natural, either in origin or character. The soil is peculiar—indeed, it is not "soil" in the narrower sense, because it contains little or no *humus* (decaying remains of plants)—and can only be colonised by a certain selection of species—mostly, though not wholly, the weeds of roadsides or of ploughland. But these species and their powers of colonisation and relative persistence furnish ecological problems of considerable interest. Broadly they behave in much the same way as the first colonists of "natural" dry areas in which there is little or no humus. Where there is much combined nitrogen derived from organic refuse, special kinds of plants will occupy the ground, of which the common stinging nettle is a good example. These *nitrophilous* plants are often specially luxuriant about farmyards, the lairs of cattle, and similar places.

Even when a habitat owes its existence directly to human activity, it may be occupied by a perfectly natural plant community, i.e. a collection of plants whose composition owes nothing to human agency, and might equally well occur in a "natural" habitat. Thus the stones of a wall built of limestone blocks will be colonised by just the same lichens and mosses that cover the surface of natural limestone rocks, the crevices by the same flowering plants and ferns that we find in the fissures of the same rocks. And similarly with a wall of sandstone, or dolerite, or granite. An artificial pond will be invaded by much the same plant communities arranged in much the same way as a natural lakelet on the same soil and in the same surroundings, a canal by the same communities as a sluggish river, and so on.

From all of which we draw the very obvious conclusion that it is not the activity of man at large that is significant to the plant ecologist, it is the actual conditions which he brings about. If human activity destroys a large number of plant communities and plant habitats, and modifies, to a greater or less extent, many more, it also produces fresh habitats and fresh plant communities, and thus provides fresh opportunities for ecological study on every hand.

PART II

STRUCTURE, DISTRIBUTION AND DEVELOPMENT OF VEGETATION

CHAPTER III

THE UNITS OF VEGETATION (PLANT COMMUNITIES)

SINCE plants are, for the most part, gregarious in their occurrence, we can never get any deep insight into their "household affairs" unless we consider them as members of the communities in which they naturally grow. The "ideal" method of study might be to investigate each species separately, till we knew in detail its life history, the methods by which and the rate at which it could spread, its behaviour under different conditions of climate and soil, and only when we had obtained this knowledge proceed to study the species as it existed in communities along with other species.

This ideal method is, however, quite impracticable. To obtain anything approaching such a complete knowledge of the ecology of any one species would mean many years of observation and experiment entirely devoted to that one species, and it is a fact that we have not yet approached to such a knowledge of any single species. It is very much to be desired that those who have the time, opportunity, and taste for such detailed and thorough *autecological* studies should undertake and carry them through. As a result of such work we should be in a very much better position to attack the problems raised by the various plant communities

than we are at present. Careful and thorough work of this sort is indeed one of the greatest needs of ecology. Some suggestions as to the lines on which it can best be pursued will be found in a later chapter.

Meanwhile we need not and cannot wait till such work has been done before tackling plant communities themselves. There are many things we can find out about the communities before we possess an exhaustive knowledge of the autecology of the individual species which compose them. Indeed, the study of a community is one of the best ways of suggesting the most important problems presented by the individual species of which it is made up. The study of a plant community always and necessarily drives us back to the individual species, and we begin to realise at an early stage how little we know about them. In this way our interest in purely autecological problems is most likely to be aroused and sustained. No apology therefore is needed for beginning with *synecology*. It goes without saying that it is essential to be able to distinguish and name accurately the species of which the communities to be studied are composed.

Plant Communities on a Country Walk.—If we take a walk through the English country-side and attend to the vegetation around us, we shall be able to distinguish without difficulty the purely artificial or culture communities, such as cereal, root, mustard, or clover crops, plantations of larch or spruce, from the natural and semi-natural vegetation of various grades. The exact degree to which these latter have been determined or affected by man may be a matter of more difficulty.

The field or meadow through which our footpath leads (permanent pasture or hay crop) is obviously mainly so determined, though the plants may all be genuine natives. Here we have an example of a plant community determined by man and dominated by different species of grass.

The copse which we presently pass has a different status. It may have been planted, but it may be a modified remnant of primitive woodland. The dominant trees and shrubs are very likely those which would have been there in any case, though their form and perhaps their relative proportions have been determined by felling and coppicing. The copse, then, is likely to be a modified example of the natural forest community, dominated very probably by oak and hazel.

Presently we come out on to a stretch of heath. This is very likely determined by a difference of soil corresponding with a distinct geological formation, for instance a sand. It may be kept in its condition as heathland by pasturing or burning, or both, and this may be evidenced by the birches, and possibly oaks, which grow on its edges, and by the patches of scrub or single bushes dotted about it. These may represent the efforts of woody vegetation to reconquer the ground, efforts which would soon be successful if it were not for the constant attacks of grazing animals. On the other hand, the soil may be unsuitable for tree growth, as shown by the yellowing and dying of young oak seedlings. The heath, then, is certainly a natural or semi-natural community, quite distinct from the meadow and the copse. It may be a stage in the development of forest, or it may represent the only type of vegetation the particular soil and climate would produce.

In wet hollows of the heath there may be collections of species different from those of its general surface, for instance the waxy heath, the purple moor grass, and perhaps bogmoss, butterwort and sundew. Here is another distinct community, evidently determined by the wet soil, and also, as we should learn by further comparison, by the very acid soil water.

Beyond the heath area we will suppose the ground slopes down to a riverside, bordered by a belt of fen or marsh, liable to be flooded by the river after heavy rains. The fen

or marsh represents yet another plant community, covered with species of grass and sedge, among which may be many other plants, which only grow in wet places, but distinct from the plants of the wet hollow in the heath. The soil of the fen or marsh may contain the same amount of water as that of the wet heath, but it is not acid, and supports quite a different vegetation.

The edge of the river itself may be lined by a reed swamp, composed of tall grasses, sedges, or bulrushes, and in the water are other plants, with floating leaves if the stream is sluggish; and others, again, wholly submerged. All these last-mentioned communities are essentially natural, though they may be modified by human activity in various ways.

It is very easy to see that the various units of vegetation are not all of equal rank. Thus within an oakwood you may have a localised belt of ashes or alders following the banks of a stream, or a patch of bluebells in one place and not in another; on a heath you have local patches of a species of grass or of moss. And clearly you cannot consider the lichens covering the bark of the trees in a wood as equivalent to the woodland itself. Yet all these are units of vegetation. We apply the term PLANT COMMUNITY to any such unit of whatever size or rank. Thus the deciduous forest of Western and Central Europe is a plant community, and so are the submerged water plants in a pond, or the green coating, often largely or entirely composed of the minute alga *Protococcus*, on a damp wall or tree-trunk. *A plant community is any collection of plants growing together which have as a whole a certain individuality.*

The Plant Association.

The fundamental unit of vegetation, the type of plant community from which we start, is the PLANT ASSOCIATION. It is as difficult to *define* an association as to define a species of organism, but most ecologists are now in fair agreement as to what communities should be regarded as associations.

Associations are, on the whole, large units, with wide extension, though this may be, and practically always is, interrupted by the occurrence of other associations. All the communities noted on our country walk are associations —or rather particular examples of associations.

Dominant Species.—In closed vegetation, where the ground is continuously covered, or continuously shaded, by plants, the association has one or more—usually more than one—*dominant species*, which mainly determine the "look" or *physiognomy* of the association. This physiognomy is primarily determined by the "life form" of the dominants, e.g. the deciduous tree, the needle-leaved tree, the heath plant, the reed form, etc.[1] Thus the common beech (*Fagus silvatica*) and the oaks (*Quercus sessiliflora* and *Q. robur*) are the principal dominants of the great deciduous forest association of Europe, the common ling or heather (*Calluna vulgaris*) is the main dominant of the heath association of Western Europe, the common reed (*Phragmites communis*), the lake reed (*Scirpus lacustris*), and the bulrushes or reed maces (*Typha latifolia* and *T. angustifolia*), are the main dominants of the reed swamp association of European fresh waters. The presence of the dominants strongly influences and sometimes largely determines the rest of the species belonging to the association, very often because the latter have to grow under the shade of the dominants, sometimes because the growth of the dominants produces a special kind of surface soil (humus), composed of its decaying parts, or otherwise reacts on the soil character.

Floristic Character.—All species other than the dominants may be called *subordinate* species. A well-defined association contains species which are either (1) confined to it,[2] (2) seldom met with outside it, or (3) at least found more often within than outside the association. Such species are said to be *characteristic* of the association. Species which are present in every example, or nearly every example,

[1] Cf. Appendix, p. 197. [2] "Exclusive" species.

of an association, whether they are met with outside or not, are called *constants*. Species which occur as often outside as within the association, and those which occur quite rarely and casually within its limits, are sometimes called respectively *indifferent* and *casual* species.

The constants of an association can be determined by comparing the complete lists of species from a sufficient number of examples, the characteristic species only by comparing the lists with similar lists from other associations. The complete list of species (determined by putting together the lists from a great number of different examples) gives the *floristic composition* of the association for the area from which the examples are taken, and the association is characterised floristically first by the dominants, secondly by the constants, thirdly by the characteristic species, and fourthly by the complete floristic composition. The *floristic character* of an association, which we may distinguish as its first character, depends on all these.

Life Form and Habitat.—The second character of an association of plants depends on the *life forms*, first of the dominants, and secondly of the various subordinate species. The life form of the dominants, as we saw, determines in the main the physiognomy of the vegetation. But it is also an index of the *habitat* (which we may call the third association character), because certain dominant life forms always go with certain habitats. (See Appendix, pp. 197–9.)

Climatic, Edaphic and Biotic Factors.—The association habitat is defined in the ecological sense as *the sum total of the conditions of the environment which are effective in determining the existence of an association on a given area.* Thus the characteristic life form of "summer forest" is the deciduous tree which drops its leaves in the autumn and produces a fresh crop in the spring. The existence of the beech-oak association of Europe and the parallel associations of eastern North America and of eastern Asia is determined by the particular climate of these regions. This

climate is marked by a warm, but not too dry a summer, favourable to the functioning of the rather delicate leaves of the deciduous forest trees, and by a winter when the soil is often too cold for the active absorption of water by the roots. If the leaves remained during the winter the tree would be killed as a result of water loss by evaporation through the leaves. On all the more favourable soils, therefore, within the area of this climate, except in situations exposed to the more violent winds, and in the absence of other adverse factors, deciduous summer forest is the natural type of vegetation.

But on the soils and in the situations unfavourable to the growth of deciduous trees other associations take their place. On such areas factors of the habitat other than the *climatic factors* come into play; for instance, soil or *edaphic*[1] *factors*, which determine the existence of other associations, e.g. pine forest, heath, reed swamp. These three are associations characterised by quite different dominant life forms, the first by needle-leaved trees, the second by heath plants (evergreen undershrubs), and the third by plants with the tall unbranched "reed type" of shoot, and rhizomes creeping in the mud, or sometimes floating in the water.

A third class of factors, *biotic factors*, are those due to organisms, and when directly or indirectly due to human activity give rise to the communities of semi-natural vegetation discussed in Chapter II.

The nature of the habitat is thus the third great character of an association. The ecological conception of a habitat includes *all* the effective factors, climatic, edaphic, and biotic alike, which determine the existence of an association in a given place. But a given type of climate determining an association like the deciduous forest is, as a rule, far more widely extended in great continuous areas on the earth's surface than the variations of soil and soil-water which determine associations like reed swamp, or the condi-

[1] Greek ἔδαφος (edaphos), the ground.

tions of constant pasturing or burning, which determine associations like our English chalk pasture, or many of our heaths. The vegetation of the earth's surface can be mapped out into great *climatic types*, each represented by *climatic associations*, corresponding more or less closely with areas of uniform climate. Within these areas various edaphic factors determine the existence of *edaphic associations*, and these are not necessarily limited by climatic boundaries. In both types of association we have to recognise the determining or *master factors*, whether climatic, edaphic, or biotic, which delimit one association from a neighbouring one. For instance, a reed swamp on the edge of a river is adjoined by a strip of pastureland: above this on a gently sloping hillside is oak forest. The master factor of the habitat which separates the pasture from the wood is biotic, namely the pasturing, which prevents the seedlings arising from acorns falling in it from growing into trees. The master factor which differentiates the reed swamp from pasture and forest alike is the high-water level at the edge of the river. The general features of the climate (rainfall, humidity of the air, temperature, etc.) permit the existence of the three associations, which are thus differentiated by biotic and edaphic factors.

Further consideration of the relations of habitats to associations will be given in the next chapter, when we have dealt with the principles of *succession* or change of vegetation on a given area.

The Plant Consociation.

The community formed by a single dominant species of an association to the exclusion of the others is called a *consociation*.

When, as is usually the case, an association has more than one dominant species, these may be mingled together, i.e. *co-dominant* (e.g. oak and beech in the European deciduous forest, sugar-maple and American beech in the deciduous

forest of the eastern United States). On the other hand, they may be separate, each dominating certain areas of the association, and forming, for instance, a pure oakwood or a pure beechwood. This separation may be due to minor variations in the habitat, some parts of which may be rather more suitable for one dominant, and some parts for another, while other areas again are intermediate, showing no great preponderating advantage for one or the other, so that mingling of the dominants or co-dominance occurs. Sometimes one of the dominants may completely occupy an area so as to exclude the others, although the habitat is equally suitable for all. This may be often due simply to the fact that the occupying dominant got there first.

Thus an oakwood and a beechwood are different consociations of the beech-oak association of Western Europe, a bulrush swamp is a consociation of the reed swamp association, a heath dominated by the purple heather (*Erica cinerea*) is a consociation of the heath association, and so on.

If a given consociation dominant flourishes best in a slightly different habitat from the dominant of the other consociations of the association, or if its presence brings about special changes in the habitat, the subordinate species of the consociation will probably differ more or less from those of the other consociations. Thus the deep shade of a beechwood tends to exclude shrubs from the undergrowth and also many herbs of the ground flora which occur in an oakwood, and the peculiar humus is apparently associated with the occurrence in a beechwood of certain other species which are not found, or are less commonly found, in oakwoods. Nevertheless, if one considers a sufficiently large number of beechwoods and a sufficiently large number of oakwoods over a wide enough area, the differences in the shrub and ground floras are scarcely sufficient to separate beechwoods and oakwoods as different associations, though

this is sometimes done. And there are many forests in which beech and oak exist side by side, though beech is excluded from some habitats (heavy wet soils) which oak can occupy, and oak from some very shallow soils which beech can colonise.

Similar considerations are true of the consociations of the reed swamp and heath associations. The lake reed (*Scirpus lacustris*) and the bulrush (*Typha*) tend to occupy deeper water than the common reed (*Phragmites communis*), and certain subordinate species tend to predominate in the deeper, others in the shallower water, but the three dominants are often mixed, and most of the subordinate species show no very clear distinction as between the different consociations. Again, the purple heather (*Erica cinerea*) prefers sunnier and drier situations—perhaps also soils with a higher mineral content—than the common ling (*Calluna vulgaris*) often inhabits; but the two very commonly grow mixed, and the subordinate species scarcely differ on the drier heaths. The ling, however, has a much wider distribution, and often inhabits much damper soils, where some of its associates are distinctly different.

The technical name of a consociation is formed by the stem of the genus name of the dominant with the suffix *etum*, followed by the name of the species in the genitive case: thus the beech consociation is *Fagetum Fagi silvaticæ*, shortened to *Fagetum silvaticæ*; the ling and purple heather consociations are *Callunetum vulgaris* and *Ericetum cinereæ*, and so on. Where there can be no possibility of mistake about the species, the consociations may be simply called *Fagetum*, *Callunetum*, *Phragmitetum*, etc.

The Strata or Layers of the Association.

The great majority of associations, all those in fact whose dominants are tall plants, have distinct *strata* or *layers* of vegetation below the dominant stratum. Thus an English wood commonly has as many as four strata:—(1) The tree

stratum, (2) the shrub stratum, (3) the herb stratum, (4) the moss stratum. Some woods have two herb strata—a tall and a short—and tropical rain forest may have six or seven distinct strata of vegetation.

Each stratum has an environment or habitat which differs from that of the others. Thus the crowns of the trees of a wood are exposed to full sunlight, and often to considerable wind, while all the other strata are more or less protected from both. The protection increases as the soil level is approached, so that the shoots of the lower strata are not only increasingly shaded, but are surrounded by a damper atmosphere, and enjoy a more equable temperature. The roots of the different strata also often have very different environments. Thus the tree roots may occupy partly the soil and partly the subsoil, or the cracks in the surface layers of underlying rock where this is near the surface; the roots of the herbs may be partly in the soil and partly in the surface humus; while those of certain herbs and the rhizoids of the mosses are confined to the surface humus.

A herbaceous marsh or fen community has commonly at least three strata—the uppermost consisting of the tall dominant grasses or sedges, at least one intermediate stratum of herbs, and a lowermost stratum of mosses and liverworts. The roots of the different strata (or of different species whose shoots are in the same stratum) may occupy different layers of soil, with, for instance, very different air and water contents. A grassland community is similarly stratified. In a comparatively damp climate like that of Great Britain the lowermost stratum of many communities often consists of mosses.

The different strata of an association are in a certain sense distinct communities. Each has a floristic composition, dominants, and a "structure" of its own; and the species of each often belong to quite distinct life forms. Each stratum has a habitat which differs, in certain respects widely, sometimes totally, from those of the others. Thus

the different strata must always be considered separatel in ecological study. On the other hand, the structure an often the existence of the lower strata depends upon th existence of the upper ones. The shrubs of a wood wi be much less dense than if the trees were absent. The shad species of the herb stratum may not exist if the trees an shrubs are absent, and may be replaced by quite a differen community. Thus the different strata of a plant associa tion are to some extent comparable with "social strata, classes, or castes of a human community, for we find th same differences of habitat within the common habitat o the whole community, and a similar dependence betwee one and another. Each requires separate study from th sociologist, but the whole community to which they belon forms the essential primary unit alike in human population and in vegetation.

The Seasonal Aspects of an Association.

In a climate with well-marked yearly seasons differen species of an association come to the height of their vege tative growth, flower and fruit, at different periods of th growing season. These activities of different species ar scattered throughout the whole season, but the species tenc to fall into distinct seasonal groups. In the British deciduou woodland, for instance, there are four such seasonal group of species, and the flourishing of each gives a distinc seasonal *aspect* to the association. Thus we can distinguisl (1) the *prevernal aspect* of early spring (March and the firs half or two-thirds of April in southern England [1]), markec by the coming into prominence of such plants as the celan dine (*Ficaria verna*), the wood anemone (*Anemone nemo rosa*), and the primrose (*Primula acaulis*): in (2) the *verna aspect* (end of April and May), the trees come into leaf anc

[1] These times are of course only approximate, depending as they do, not only upon the latitude, altitude, soil and exposure, but also on the weather of the particular season, especially in the spring.

flower, and in the ground vegetation the bluebell (*Scilla nutans*), stitchwort (*Stellaria holostea*), weasel snout (*Galeobdolon luteum*), etc., develop: in (3) the æstival or *summer aspect* (June–August), a number of other species become prominent; (4) the *autumnal aspect* (September–November) shows very few or no fresh flowering plants in the woodland, but is marked by the appearance of many fungi. Many species extend their activity above the soil through two or more aspects.

We must be careful to distinguish the growth and activity of the leafy shoots of a plant from its flowering, though these are sometimes contemporaneous. The hazel (*Corylus avellana*) flowers in the prevernal aspect, but its leaves do not appear till the vernal. The dog's mercury (*Mercurialis perennis*) flowers in the prevernal or early part of the vernal aspect, while its leaves are active in the prevernal and vernal and right through the summer aspect. The meadow saffron (*Colchicum autumnale*), on the other hand, produces its leaves in the prevernal aspect, but its flowers do not appear till the autumnal, long after the leaves have disappeared. Under the different aspects we have therefore to note what plants are in a state of vegetative activity, as well as what plants are in flower.

Deciduous woodland is characterised, in its ground strata especially, by its rich prevernal and vernal vegetation, though it also contains many æstival species; grassland is mainly vernal and æstival, but is active to some extent throughout the year according to the weather; while heath, fen and salt marsh are essentially summer vegetation continuing into the autumn.

The Plant Society.

Within an association or a consociation certain gregarious subordinate species form communities of lower rank. These *local* communities are called SOCIETIES. Examples are societies of wych elm in an ashwood, of ash or alder in the

damper parts of an oakwood, of *Brachypodium pinnatum* on the chalk downs of south-eastern England, of the moss *Polytrichum* on heaths, etc.

A society has usually a single dominant, which may occupy the ground to the exclusion of the association dominants. Sometimes the subordinate species within the limits of the society differ markedly in relative frequency from those of other parts of the association. Thus a society of a tree, such as the sycamore, casting heavy shade in an oakwood, will reduce or cut out many of the species common under the lighter oak-canopy. Sometimes subordinate species occur in a society which are not present or are quite rare in other parts of the association, for instance the moschatel in the societies of dog's mercury in the Derbyshire ashwoods. This is due to the fact that the society dominant only occurs in those parts of the association where the habitat is locally different (*habitat societies*), or it may be owing to the fact that the growth of the society dominant itself creates new local conditions which lead to the great abundance of certain subordinate species, or to the appearance of others not found elsewhere in the association.

The society dominant is a subordinate species when we consider the association or consociation as a whole, but within the society the other species may be subordinate to it. A society, as has been said, is " a dominance within a dominance." When highly organised, it gives a repetition of the structure of an association in miniature.[1] The most slightly organised (lowest) form of society is represented by a mere local dominance of a subordinate species of the association (sometimes due to a chance aggregation of seedlings in one place, often to social vegetative growth) without change in the average distribution of the other subordinate species, except in so far as the social species excludes others

[1] Such societies may really represent fragments of some distinct association, as in the case of patches of heath on sandy banks in a wood.

by mass growth. The most highly organised type of society (approaching the character of an association) is represented by a characteristic list of subordinate species differing from that of the association at large (e.g. the society of *Juncus effusus* on the wetter parts of grassland or heavy soil; of *Erica tetralix* on the damper parts of heaths, etc.). Such a characteristic list can, of course, only be established by comparing a large number of examples of the same society.

Stratum Societies.—Societies of a stratified association may involve all the strata, i.e. every stratum may show, within the society, different frequencies of the species of the stratum, and perhaps some different species from the rest of the association. This occurs, for instance, in a wood where the dominant tree of a society has a marked effect on the habitat by casting greater or less shade, or by producing a different kind of humus from the consociation dominant. But other societies may be confined to one or two strata, e.g. the herb stratum, or the herb and moss stratum of a wood; or, again, the shrub stratum alone, e.g. societies of hawthorn. Societies not involving all the strata may be called *stratum societies.* The ground societies of woodland are often numerous and varied, and may or may not be correlated with the habitat conditions. It has been shown in the case of a Cambridgeshire wood **(32)** that the societies of dog's mercury, of wild strawberry, and of meadow-sweet are closely connected with the summer water content of the soil, and to a less extent with light. In Hertfordshire woods **(43)**, societies of bracken fern and wood anemone, of lesser celandine, dog's mercury, etc., have been shown to depend on soil moisture, humus content, and soil acidity.

"Aspect Societies."—Societies confined to one seasonal aspect of an association are sometimes called "aspect societies." But when a given patch of ground is occupied by the shoots and leaves of one or more species in one aspect (e.g. the prevernal), and by quite other species in another (e.g. the æstival), we must be careful how we refer to these

as two different "aspect societies," for we must remember that the underground parts of the species not in evidence on the surface during one aspect are nevertheless present all the time, and may influence the development of the species that happen to be conspicuous at the moment. A society composed of species whose aerial parts vegetate actively in different seasons or "aspects" has been called a "seasonally complementary society." Each case must be decided on its own merits. The criterion of a distinct community is relative independence.

Units of Semi-natural Vegetation.

Vegetation which owes its existing form to human activity, though not actually sown or planted by man, shows the same classes of units as purely natural vegetation, and can be treated in just the same way. The human activity in question—burning, pasturing, mowing, etc.—has to be taken as one of the constant factors of the habitat—indeed, as the differentiating or *master factor* (see p. 34). It does not follow, however, because a heath, for instance, is periodically burned that it would be anything but a heath if it were not burned—each case must be investigated on its own merits to ascertain what effect in modifying or altering the vegetation the particular human activity actually has.

Even when the habitat is entirely artificial, deviating widely from anything in untouched nature, the same treatment can be followed. In such habitats, however, the vegetation is very often *young*, i.e. it has not attained a position of relative equilibrium, and to treat it intelligently the observer must understand—as, indeed, he must with all vegetation—the principles of *succession*, i.e. the sequence of changes which vegetation undergoes on a given area. These are dealt with in the next chapter.

CHAPTER IV

THE SUCCESSION OF VEGETATION

LIFE never stands still: it is everywhere in a continuous process of flux and change. In the last chapter the units of vegetation were treated as if they were static units, with a definite, fixed composition, structure and habit, but in reality they are constantly changing. We must in the first instance define the natural units which are actually formed in the course of the changes of vegetation in order to have something to work with. Broadly, we may regard these units—our associations, consociations and societies—as representing positions of relative equilibrium into which plants group themselves. Some are more stable, others less stable: some, that is to say, remain essentially the same things for a long time, for centuries or perhaps for many thousands of years, others are very transient, giving place in the course of a few seasons to other communities, of different composition. Sometimes the change is fluctuating, the different species being here to-day, gone to-morrow, and back again the next day, so to speak. This is especially seen in the annual and biennial vegetation of open soil, sand dunes, roadsides, waste places, neglected garden beds, etc.

But besides this fluctuating change, there can generally be observed, through a series of years, a definite trend in one direction towards a position of equilibrium. All such progressive change is called *succession*.

We must at the outset distinguish two classes of change, which bring about the succession of vegetation. If an area of ground is bare of vegetation, or if new bare ground is

formed—as by emergence from the sea, by the drying up of a lake, by deposit of alluvium by a river, by the retreat of a glacier, by a deposit of wind-blown sand, by the fall of talus from a cliff, etc.—plants will, in the great majority of cases, begin to occupy it sooner or later. The first species to occupy the area will, however, in most cases give way to others, and these again to others, until a state of relatively stable equilibrium is reached between the vegetation and its habitat. This kind of succession is called the *development of vegetation.*

But change may also be brought about by continuously acting outside factors which are constantly altering the habitat, thus making it less suitable for the first occupants of the ground and more suitable for others, as for instance a gradual change of climate, the gradual silting up of a lake, the increasing concentration of salt in the soil as an inland sea dries up, the "leaching" (gradual washing out) of soluble salts from the surface layers of a soil by the percolation of rain-water. All these changes, which are independent of the plants, gradually alter the habitat, and thus bring about changes in the vegetation.

In pure *development* the habitat also changes, but it is by the *reaction* of the plants upon it. As the individuals die the products of their decay accumulate as *humus* in the surface layers of soil, altering its physical structure and chemical nature, and increasing its water-holding capacity. Thus the habitat is usually rendered more favourable to plant life, and species which make higher demands on the soil than the original pioneers are able to obtain a footing. In general, bigger plants progressively replace smaller ones; and in all the more favourable climates of the world, on the more favourable soils, woody plants come to occupy the ground, and forest vegetation is ultimately established. As the vegetation becomes closer and taller the shelter increases and provides a habitat for subordinate species which could not enter the earlier communities.

Of course, these two kinds of change are not necessarily eparated in natural successions. Developments are often nodified by concurrent changes in external factors. For nstance, the development of aquatic reed swamp and marsh regetation on the edge of a lake may be modified by the leposition of silt brought down by streams **(37)**. This can be shown to alter the course of development, i.e. to lead to he formation of communities differing from those which vould have appeared if there had been no silting. But it s important to keep clear in the mind the distinction between he two classes of factors which influence succession. An nstance in which the latter alone is at work is the effect of a gradual continuous change of climate on a plant community. Thus, a forest which represents the culminating stage of development for a certain climate at first existing, and is thus in relatively stable equilibrium with its habitat, nay alter in composition, or disappear altogether, to be replaced by some other type of community, as the climate becomes, for example, progressively drier or colder.

The early course of development of vegetation on bare ground differs entirely according to the nature of the initial habitat, in the first place whether it is submerged or exposed to the air, and if exposed whether it is wet or dry; for the plants which can colonise such different habitats differ very widely. On submerged ground, as in the shallow water on the edge of a lake or pond, we have the series: submerged aquatic plants, aquatic plants with floating leaves, reed swamp plants. As the soil level is built up by accumulation of plant remains, or by silting, or by both together, till it reaches the surface of the water, fen or marsh will succeed reed swamp. Shrubs and trees which can tolerate waterlogged soil round their roots (in this country such trees as alder, willows and birch) often follow, and as the soil level is built higher above the water-level by accumulation of humus, the climatic forest association may complete the series.

On a dry, bare habitat, such as an exposed rock surface, the talus from cliffs, etc., the early stages are totally different. Lichens and terrestrial algæ, together with rock mosses—plants which can themselves hold rain-water—are the pioneers. These begin to disintegrate the surface of the rocks, and with the decayed parts of their own bodies form a very thin soil. This is colonised by other mosses which form thicker cushions, and the soil gradually increases enough to support herbs whose roots can do with a thin soil. Then, as the soil grows thicker, more strongly rooting herbs appear, and after a time the seedlings of shrubs and trees take a hold. Eventually, with the thickening layer of soil and humus, comes the climatic forest association.

On the talus of cliffs the interstices between the rock fragments form an initial habitat very different from the surfaces of the fragments, and the seeds of herbs, and even of shrubs and trees, often germinate in these interstices and successfully establish themselves at an early stage, long before they can colonise the thin soil formed by the lichens and mosses on the rock surfaces. This depends partly on the weathering of the rock and how much mineral soil is formed by disintegration and washed down into the interstices, and partly on how much humus is carried down by rain from the surface vegetation. On a talus formed of small fragments—gravel, down to the size of coarse sand—the succession is much quicker and herbs play the leading part as pioneers, binding the loose gravel, forming mats on its surface and comparatively quickly producing a suitable soil for the establishment of shrub and tree seedlings. On damp sand or silt, such as is laid down by a river in flood, colonisation and succession is still quicker, owing to the relatively favourable soil that is presented to the plants from the outset: herbs or even shrubs and trees begin to colonise the area at once.

The early stages of the development of vegetation thus vary quite definitely according to the nature of the initial

habitat, and this influences the course of succession for a considerable time. The *tendency* is always ultimately to develop the most complex association with the largest dominants that the climate permits, whatever that may be, and for this reason such an association is often called the *climax association*, because it represents the final pitch of development which the particular climate allows.

The climatic climax, however, as we saw in the last chapter, is not developed on all areas within the corresponding climatic region. The nature of the soil, the presence of permanent bodies of water above or nearly reaching the ground-level, as well as other local but constant physical factors of various kinds, may altogether prevent it, and so may the existence of a permanent human factor like pasturing or periodic burning. Hence development of vegetation may be arrested at some stage of the succession which has been called a *sub-climax*. Thus the development to climax forest may be arrested in the stage represented by grassland or heath by constant pasturing or repeated burnings. The grassland or heath is then a sub-climax. The arresting factors not only stop development, however, they frequently *modify* it considerably. It is better, therefore, to consider all *relatively permanent* associations as *climaxes* of development, i.e. the furthest points attained under the action of the particular factors at work, whether these are climatic, edaphic or biotic (due to climate, to soil in the wide sense, or to animals).[1]

[1] The distinguished American ecologist, F. E. Clements, who has worked out a detailed theory of the development of vegetation in his large work *Plant Succession* (Carnegie Institution of Washington, 1916), regards only the climatic associations as climaxes, and confines the term " association " to those. He recognises *sub-climaxes* in which development is arrested before the climatic climax is reached, and *post-climaxes*, i.e. local communities developed where specially favourable soil enables vegetation to reach a more highly developed stage than the climatic climax of the region, for instance deciduous forest along watercourses in arid regions where the climatic climax is dry grassland. Any particular series of developmental communities he calls a *sere*, and he uses the termination *-es* for the names of seral as

In a country like Great Britain, where man has modified the spontaneous vegetation so that most of it is what we have called "semi-natural," we can rarely find those long series of stages of development from bare habitats to the climatic climax which we have outlined above, and which we can study in regions of the world approximating to the virgin condition. We find instead a patchwork of communities, from the pioneer communities of bare areas to the climatic climaxes, nearly all modified in various ways by man or his animals, and mixed with areas of sown or planted crops. All of these, if left to themselves, would progress towards the climatic climax on the more favourable soils, or to some edaphic climax on special types of soil; but man is constantly stopping or modifying the development or throwing it back to some earlier stage. Where he has introduced a more or less permanent modifying factor or set of factors, we have biotic (anthropogenic) [1] climaxes or some stage of development towards them.

All development of vegetation initiated, not on new ground, but by some modification or destruction of pre-existing vegetation, is known as SECONDARY SUCCESSION, and it is with secondary successions that we have mainly to deal in a country like our own. Its course is necessarily different from that of primary succession on new ground, because the starting-point is different and the time occupied to complete it is less. Instances are the clear felling without replanting of a wood, or the burning of a heath. The secondary successions (or *subseres*) most like primary successions (*priseres*) are those which are started by complete destruction of the original vegetation and its soil, as when stone is quarried or gravel dug, and the gravel pits or

opposed to climax communities. Thus a seral community of the rank of an association he calls an *associes*, of the rank of a consociation a *consocies*, of the rank of a society a *socies*. Some British ecologists are beginning to use these terms, but they are not yet generally adopted.

[1] Produced by man, from Greek ἄνθρωπος, man, and the root γένω, produce.

quarries are afterwards abandoned. In such cases the original soil is completely destroyed, and the colonisation begins on bare rock or on a loose but purely mineral surface. A parallel case in the water succession (*hydrosere*) is the digging of an artificial pond.

It is obvious that the colonisation of new ground or of bared or partially bared ground must depend on the species of plants available to colonise it. This involves three factors: first, the actual proximity of seed or spore parents; secondly, the means of migration, i.e. the methods by which the seeds or spores are carried (wind, birds, etc.); and thirdly, the suitability of the habitat for the successful germination and establishment of the young plants.

The first colonists of dry areas (terrestrial algæ, lichens, mosses) are widely distributed plants whose spores are carried considerable distances by the wind. In a sufficiently damp climate they arrive and establish themselves quickly, in a dry one much more slowly. The herbs which usually come next are frequently annual species (often weeds of way-sides and arable land) with light seeds or structures which aid dispersal by wind (hairs and plumes attached to the seed or fruit). They grow quickly, their life is very short, and they do not make great demands on the soil. They form transient communities, which often shift from place to place from year to year. The later-arriving perennial herbs appear more gradually, frequently because their means of transport is not so good, so that they come a few only at a time at longer intervals. They also commonly germinate more slowly, and require for germination more moisture, so that seeds which arrived too early and fell on the surface of raw soil without humus would not grow into plants.

Finally, many of the trees and shrubs require much more favourable conditions, especially a *deeper* soil, for successful germination and establishment, so that they have no chance in the conditions of the habitat during the early stages of development (except for instance in the interstices of talus).

And here the actual proximity of the seed parents becomes a very important factor in a country like Great Britain, where man has long ago destroyed most of the forest to which its climate is suited. The great distance of seed parents from many areas which could be colonised by trees if seed were available, combined with the poor means of dispersal of the climax dominants, oak and beech, is sufficient to account for the rarity of natural colonisation of many suitable areas by these trees. Ash and birch have winged fruits, and come quicker over the country generally, while pine, which has winged seeds, often comes very freely if pine woods or plantations are not too distant.

The earlier communities of bare ground are *open*, the individuals scattered here and there with stretches of bare soil between: the habitat is not fully occupied. They consist of comparatively few species, those fitted to cope with the special conditions of life in such situations—the lack of humus, the exposure, the frequent dryness of the surface layers of soil.

The later communities become more and more *closed* (except where the soil or climate is very unfavourable, in which case the climax is an open association, as in a desert), the individuals more numerous, and the number of species increases, as the habitat becomes more favourable for a greater variety of plants. Certain species become dominant, at first locally, and finally the dominance of a few—often only one or two—is established. In some climax associations, however, for instance many grasslands, the dominance is shared by several species, generally of the same life form. The community becomes definitely layered, species which can only exist in good shelter appear in it, and the final structure comes into existence. When this is once established it is difficult for new species to enter the association.

All these features give a stable definite structure to a climax community and contribute to its strong individuality.

CHAPTER V

OUTLINE OF BRITISH VEGETATION

At this point we may usefully introduce a summary outline of existing British vegetation,[1] in order to give the beginner some idea of the material at his disposal.

In Great Britain we have a varied assemblage of plant communities, most of them more or less modified, and many created by man. A certain number, however, notably many of the freshwater communities, the seaweeds, the maritime vegetation of sand dunes, shingle beaches and salt marshes, the vegetation of sea cliffs, and of some of the remoter mountains and moorlands of the north and west, are but little, if at all, influenced by human agency; that is to say, they would have been just the same, so far as we can tell, if man had never inhabited this island. But they are all, whether entirely natural, semi-natural or artificial, open to ecological study.

Deciduous Summer Forest.—The climatic climax of the plains, the valleys and the lower hill slopes of England, Wales and southern Scotland, as well as a large part of Ireland, is the deciduous summer forest association of Western and Central Europe. In the British Isles it is dominated mainly by the two deciduous oaks, *Quercus robur* and *Q. sessiliflora*; and on certain soils, especially of the chalk in the south-east and of the Gloucestershire oolites somewhat further north and west, by the beech (*Fagus silvatica*). The beech is here apparently at the limit

[1] A fuller account will be found in *Types of British Vegetation* (Cambridge, 1911). This book has, however, long been out of print; it is in some respects out of date, and its theoretical basis needs revision.

of its north-westward migration, though it flourishes, sets seed, and reproduces itself freely when planted in suitable situations in Scotland and Ireland. On the calcareous soils of the older limestones of the north and west, outside the area of the beech, the woods are dominated by ash (*Fraxinus excelsior*). This ash-consociation has not been described outside the British Isles.

The other British trees which dominate widely distributed communities are the alder and the birches (see below). The hornbeam (*Carpinus betulus*) plays a certain rôle in parts of the south-east, the area in which it is indigenous being more restricted than that of the beech; and the yew (*Taxus baccata*), with a much wider distribution, is perhaps a climax dominant on some parts of the southern chalk. But it is doubtful if either of these trees can be considered a consociation dominant. The hornbeam tends to be subordinate to the oaks, the yew to the beech and sometimes to the oaks.

The native woods have very rarely been left untouched: it is probable, indeed, that no virgin wood now exists, except perhaps small fragments in some of the remoter valleys. Great areas of woodland have long ago been cleared and converted to arable or pasture. Indeed, the proportion of the country occupied by woodland, including plantations, is less than that of any European country except Portugal. In the oakwoods which remain, the shrub-layer, preponderantly of hazel (*Corylus avellana*), with other shrubs associated, is practically always coppiced. A few standard oak trees only are present, not enough to form close canopy; or the coppice is left without them. The beechwoods of the south have certainly been partly planted, probably in many cases where the tree was formerly dominant. Some, however, are in all likelihood the direct descendants of natural beechwood. Natural regeneration of oak and beech wood at present only occurs here and there, so greatly have the natural conditions been altered.

The ash, which reproduces more abundantly and dis-

tributes its fruits more widely than either oak or beech, consequently springs from seed much more often, but where pure ashwood is found within the area of native beech it is generally to be regarded as a *seral* community or *consocies* (see p. 47, footnote). The same is true of the birches (*Betula pubescens* and *B. alba*), which are, like the ash, light-demanding trees unable to grow in *full* competition with oak or beech, and which produce abundant easily scattered fruits that readily germinate to produce large crops of seedlings. In natural succession the ash commonly precedes the beech, and the birches the oaks, but this rule is not invariable. The actual relations in any given case depend largely on soil preferences—broadly the birches can range over acid, the ash prefers more basic and damp, fresh soils—as well as on distribution factors, and are too complicated to discuss in detail here.

In permanently wet places with neutral or basic soil the alder (*Alnus glutinosa*) appears to be the climax dominant, though it probably gives way to the trees of the climatic climax if the soil becomes progressively drier. Associated with it in the succession are the crack willow (*Salix fragilis*), as well as other species of shrubby willows, and also often ash and birch—the former only on neutral or basic soils. Certain alder woods, for instance in the region of the Norfolk Broads, are very probably practically virgin.

As a whole, the British woods are semi-natural, that is they are the more or less modified descendants of original natural forest. This statement does not of course imply that there are not many plantations. The greater part of these are, however, on the sites of old woodlands, and since the indigenous trees have often been planted, it becomes, in the absence of accurate historical records, very difficult or even impossible to say of any given wood that it is certainly planted or certainly the direct descendant of natural forest. A plantation of the natural dominant on its own soil will in course of time assume the characters of a natural wood.

Northern Coniferous Forest.—In north central Scotland the oakwoods begin to thin out and eventually disappear altogether. In certain places there are native woods of the true Scots pine (*Pinus silvestris* var. *scotica*). This region, and probably also the north-west of Ireland (where there are now no native pinewoods, but much pine is found in the recent peat), belongs to a climatic region distinctly different from the rest of the British Isles, namely the oceanic division of the region of north European coniferous forests, which is better represented in Norway. Associated with the pine of this region—and indeed far more widespread—are birches, more prolific in small species and varieties than the seral birches of the south. These pine and birch consociations of the north belong therefore to a different association from the deciduous forests of the south, and their subordinate vegetation is much poorer in species. Many of these are the same as those of the southern woods, the hardier species, which can stand the more severe climate, having penetrated farther north since the retreat of the ice; but the northern woods have also a few species of their own.

The common pine (*P. silvestris*), which is a very widely distributed species in Europe and northern Asia, must have grown freely in southern England in post-glacial but prehistoric times, judging from its frequent occurrence in recent deposits. In early post-glacial times the climate of southern England was sub-arctic and probably oceanic (though at a later date it apparently passed through a drier and warmer phase), and the pine remains are relics of the post-glacial vegetation before the invasion of deciduous forest from the Continent. In the seventeenth and eighteenth centuries the common pine was extensively planted in England, and on the light sandy soils it has in many places spread from the plantations and established itself in pure subspontaneous woods or among the oak and birch, particularly in Hampshire, Surrey, Sussex and Kent.[1] It is interesting to note that in

[1] A great deal of this subspontaneous pine was cleared and used for pit-props during the war of 1914–18.

Denmark and Belgium, as in England, there is now no native pine, though the species is extensively planted; but in these countries it disappeared only during the historical period.

Heath Association.

The heath association of north-western Europe is developed in wide stretches on the west coast of Ireland, in Cornwall, and even more extensively on the west coast of France; also in Jutland, Holland and north-west Germany. But the same community occurs on sandy and dry acid soil throughout the British Isles. The principal consociation is the *Callunetum vulgaris,* dominated by the common ling (*Calluna vulgaris*), which is often pure over considerable areas. The *Ericetum cinereæ,* dominated by the purple or bell heather, *Erica cinerea,* is confined to the western part of Europe. On the serpentine rocks of the Lizard, in Cornwall, and in Brittany, Spain and Portugal, there is a consociation dominated by the handsome mauve-flowered species *Erica vagans.* On some areas the heath association is represented by a consociation of *Vaccinium myrtillus,* a deciduous ericaceous under-shrub, which is often mixed with *Calluna.*

The status of the heath community—its relation to the habitat and to other associations—is different in different places. On the exposed western coasts, with their intensely "oceanic" climate, and on exposed high-lying peat moors, which are not too wet, but where trees cannot grow, it is the climatic climax. On sandy soils throughout the British Isles the heath community often occupies the ground, but here it will generally be succeeded by trees, especially birch and pine, if seed is available. Oak and beech sometimes follow. In other places it seems that forest cannot establish itself, on account of the dryness, shallowness, or acidity of the soil, though the conditions in question have not been fully worked out. If the soil really stops the succession to forest, the heath community in such cases is an edaphic association. It is certain, however, that many of our heaths are maintained

in this condition not by soil character but by burning and grazing, and here the association is biotically determined.

Callunetum requires an oceanic or sub-oceanic climate, disappearing as the Continental climate of central and eastern Europe is reached. It cannot grow on some soils, and it does not survive heavy shading, so that it is only dominant in situations and on soils where thick continuous forest cannot become established. On the other hand it often maintains itself between the trees of a birchwood, which does not cast heavy shade. Overgrazing and trampling destroy it, and, subjected to these conditions, it gives way to certain types of grassland.

Grasslands.

The great bulk of the grasslands of Great Britain, apart from the land which was formerly arable and has been "laid down" to pasture, are certainly man-made associations, almost always due to pasturing. The chief exceptions are certain maritime, sub-maritime, and mountain grass communities where edaphic or climatic factors, especially sea-salt, wind near the sea or at high altitudes, prevent the establishment of woody plants. For the rest it may be said that where grass grows, or rather where most of our meadow grasses grow, trees can grow; and that the cause of their absence is that their seedlings are eaten off and killed, while the dominant grasses of the sward, after being eaten down, constantly shoot again from buds close to the surface of the soil.

This relation of forest and grassland can be well seen on many of the English grass "commons," which still bear fragments of unfenced woodland. The part of such a common nearest a village, for instance, may be pure grassland. Sometimes it bears isolated bushes or patches of scrub consisting of spiny shrubs (gorse, hawthorn, blackthorn, bramble), which the grazing animals avoid. The grass goes right up to the edge of the wood and between the outlying trees, which cannot regenerate, sometimes

because any tree seedlings which became established would be eaten off, sometimes because the compacted soil forms too firm and dry a surface for the seeds of the trees to germinate upon. Thus the area of woodland will constantly shrink and be replaced by pasture.

Within the shade of the wood the grasses of the open common can no longer grow. If the wood is small and the grazing on the common heavy, few or no woodland species will exist, because the animals come right through it, eating off or trampling down any herbs which appear. But if it is larger and not pastured, woodland plants will be met with as soon as the marginal zone is passed; and young trees may be found where there is sufficient light and the surface soil is suitable for the germination of their seeds.

The actual communities dominated by grasses occurring on such pastured commons vary according to the soil. A widespread association of sandy soil, and of the somewhat similar soils of many northern and western hillsides whose rock is siliceous, is dominated by the common "bent" (*Agrostis vulgaris*) and the sheep's fescue (*Festuca ovina*), often with the sweet vernal grass (*Anthoxanthum odoratum*). This is a biotic (grazing) association developed where heath and then woodland would come if grazing were stopped. If the grazing is less heavy, the heaths (*Calluna* and *Erica*) are often locally or generally dominant. If the soil is distinctly acid and peaty, the silver hair grass (*Deschampsia flexuosa*) or the mat grass (*Nardus stricta*) becomes prominent or even dominant, and in damper places the purple moor grass (*Molinia cærulea*) is often dominant.

On heavier and "better" soils with a higher content of soluble salts the common meadow grasses, *Poa pratensis*, *P. trivialis*, *Lolium perenne*, *Dactylis glomerata*, etc., form good pasture. The corresponding woodland is the pedunculate oak consociation (*Quercetum roboris*). Where there is much lime in the soil the Avenæ (*Avena pratensis*, *A. pubescens*) and the allied *Trisetum flavescens* often

become prominent. On the dry soils of the chalk (and also on the older limestones) we have a closely grazed turf of *Festuca ovina* or *F. rubra* var. *fallax*, associated with a number of herbs characteristic of dry or highly calcareous soils, giving the well-known and highly characteristic association of chalk pasture.

The communities mentioned, or modifications of them, occupy between them the greatest extent of the semi-natural grasslands of Great Britain. Since they are all associations whose form and constitution is determined by grazing, they all give place to something else if grazing is withdrawn. This something else is ultimately forest, provided seed of the appropriate trees is available; but the kind of shrubs and trees that come, and the conditions under which they come, as well as the corresponding changes in the soil, require much detailed study.

The more porous soils show a general tendency, in our climate, to progressive "leaching," i.e. washing out of soluble salts from the surface layers of the soil, and this frequently leads to increasing acidity of the surface soil with a corresponding gradual change in the vegetation with lapse of time. How far and in exactly what way this external cause of succession affects the development of the vegetation to forest is a question on which we need much fuller information than we possess at present.

Freshwater Communities: Marsh, Fen and "Moss."

The next group of communities that we must notice are those developed in the succession from freshwater to land, which takes place partly by silting and partly by the growth of peat at or near the water-level.

The freshwater communities themselves, consisting partly of algæ (with mosses in some waters) and partly of flowering plants, present peculiar difficulties of classification, and no general satisfactory scheme has yet been produced. We know, however, that the richness or poverty of the water

in dissolved oxygen, in various soluble mineral salts, and also in suspended material (silt), has a determining influence on these communities.

The types of vegetation borne by the alluvial and peat land produced on the edges of freshwater (lakes and rivers) are influenced by the same factors, and we may distinguish between marshland, fenland and mossland (or moorland) according as the soil is formed mainly by silt, by peat containing considerable quantities of certain salts, or by peat very poor in these salts. Marshland may approximate to fenland or to moorland according to the abundance or poverty of salts in the silt, and need not here be dealt with separately.

Fenland occupies the upper parts of the sites of old estuaries as well as the edges of certain lakes and the alluvial soil bordering streams. It is particularly well developed in East Anglia, where the rivers largely drain the chalk and bring down "hard" waters rich in lime. The greatest area of fenland lies between Cambridge and the Wash, but this is almost wholly drained and cultivated. The smaller area in East Norfolk (the "Broads" region) is in a much more natural state.

The development of fen commonly starts from the reedswamp association, which may be regarded as the culmination of the series of aquatic communities proper. Reed swamp shows consociations of *Scirpus lacustris* (great reed), *Typha* (bulrush) and *Phragmites* (common reed), as well as smaller communities (consociations and societies) of other species, including the tall sedges (*Carex riparia*, *C. pseudo-cyperus*, etc.) and grasses such as *Glyceria aquatica* and *Phalaris arundinacea*. As the submerged soil approaches the surface of the water by the continued accumulation of organic debris from the reedswamp plants, the landward edge of the reedswamp is gradually invaded by fen plants, i.e. plants whose shoots are subaerial instead of partly submerged. The two most characteristic fen dominants are *Cladium mariscus*, a stout saw-leaved Cyperaceous plant, and *Juncus obtusiflorus*, the fen rush, though the common

reed, *Phragmites communis,* and in some fens *Glyceria* and *Phalaris,* may remain dominant so long as the water-level remains sufficiently high. The two last-named are characteristic of reed swamps and fens in which there is abundance of mineral salts in the water. Such fens are also characterised by a greater variety of dicotyledonous flowering plants. The purple moor grass (*Molinia cærulea*) becomes dominant in some fens, as they become drier and probably more acid by leaching.

The fen association, if not regularly cut, is soon colonised by shrubs and trees. Among the shrubs are *Salix cinerea, S. repens,* and other willows, the two species of buckthorn (*Rhamnus*), the guelder rose (*Viburnum opulus*) ; and the low-growing sweet gale (*Myrica gale*) ; and of trees, the hairy birch (*Betula pubescens*), the ash (*Fraxinus excelsior*), and the alder (*Alnus glutinosa*). Ultimately fen wood or "carr" is formed, typically dominated by the alder, but sometimes by the birch.

Fen often passes into moor in sufficiently wet climates by the increasing acidity of the peat as it is built up above the level of the soil water (with its dissolved salts) and the plants come to depend on rain water. The bog moss (*Sphagnum*) appears, and a number of other typical moss plants, e.g. cotton grass (*Eriophorum*). Moor, or "moss," as it is often locally called, may also, as was indicated above, directly succeed reed swamp or other aquatic communities, if the water is poor in basic salts, especially calcium carbonate. As the moss peat slowly accumulates and the surface is built up farther above the water-level, it becomes drier, and is often colonised by *Calluna.* Such a moss may in fact pass over into heath vegetation. Later the surface may be colonised by *Betula,* and come to bear birchwood. The process of drying is often accelerated by the cutting of drainage ditches, though it may take place naturally. It is retarded, perhaps indefinitely, in a very damp climate where the rate of evaporation is low. There is no satisfactory evidence that moor can develop into climax forest (oak).

Upland "mosses" are typically formed on summit plateaux covered with "till," i.e. tenacious clayey soil left by the ice sheets of the last glacial period, which over-rode the summits of the lower mountains. A very wet climate favoured the colonisation of such areas by the bog moss (*Sphagnum*), the cotton grass (*Eriophorum vaginatum*), and the "deerhair sedge" (*Scirpus cæspitosus*). Large areas on the Pennine plateaux, in north-west Scotland and in Ireland, are covered by vast consociations of one or other of the two last-named plants. On drying of the peat, whether by change of climate or the cutting back of streams into the plateau, these plants are succeeded by heath plants, the bilberry (*Vaccinium myrtillus*) or the ling (*Calluna*). Many gently sloping areas occur on the Pennines, where these plants are mixed with cotton grass. On steeper and better drained slopes the ling or the bilberry are alone dominant.

The mat grass (*Nardus stricta*) is dominant on thin peaty soils overlying siliceous rock and on the peat debris eroded from the edges of the peat plateaux. On still thinner peaty soils the silver hair grass (*Deschampsia flexuosa*) is dominant. A third species, the purple moor grass (*Molinia cærulea*), occurs where the peaty soil is well aerated by percolating (*moving*) water, and also probably where it obtains a greater supply of bases. *Molinia* frequently occurs also on the damper parts of lowland heaths, and on the edges of mosses as well as on fens. (Cf. pp. 57, 60.)

All this last-named vegetation is characteristic of the country which is called "moor" in ordinary English, and is really an *upland heath* (e.g. the typical "grouse moors"—Calluneta—of Yorkshire and Scotland). It is distinct from the much wetter *moss* (which, together with fen, would be "moor" in German), i.e. vegetation on thick peat. The type of grassland (pasture) dominated by *Agrostis vulgaris* and *Festuca ovina*, mentioned on page 57 shows transitions to heath (both upland and lowland) by the coming in of species like *Deschampsia flexuosa* on thin peat or peaty

humus, and of the heath plants proper where pasturing is reduced or abandoned. On the slopes of the southern Pennines there is fluctuation between this grassland and upland heath according to the amount of pasturing on the one hand, and on the other the tendency to form peaty humus, which is a constant factor in the moist climate (29).

The wet climate of the hill country of the north and west of Great Britain leads not only to the leaching of the surface layers of soil owing to heavy rainfall, but also to the building up of acid humus below the herbage owing to the even more important climatic factor of almost constantly moist air combined with low temperatures, which impedes the natural process of humus decay. The result is seen in the prevalence of heath and moor plants in the semi-natural pastures even on well-drained hillsides and even above limestone rock, except where "flushes" from springs or from surface drainage bring down fresh supplies of basic salts dissolved from the rocks.

With the exception of some of the higher-lying mosses, all the plant communities mentioned in the last section now occupy country which probably at one time bore forest—at lower altitudes *Quercetum sessiliflorœ*, at high altitudes *Betuletum pubescentis*, and probably *Pinetum silvestris*. Felling and grazing have no doubt been largely responsible for the disappearance of oakwood and its replacement by heath and grassland, thus depressing the upper limit of forest, and leading to the general bareness of the hilly regions of the north. Perhaps increasing wetness of the climate has led, in part at least, to the replacement of birch and pine by moss, for both these trees are to be found locally embedded in the peat. Pine rarely spreads from plantations as it does on the drier southern heaths.

The birch and pine woods whose remains are preserved in the peat may be looked upon as the southern extensions, at the higher altitudes, of the birch-pine association of north-central and northern Scotland. A fringe of birchwood still

exists in many places above the oakwoods of northern England and southern Scotland, but pine is no longer indigenous except in Scotland.

Arctic-Alpine Vegetation.

While the rounded tops and summit plateaux of the hills whose altitude is round about 2,000 feet are mainly occupied by the moor or moss communities, many of the higher mountains, especially in the Highlands of Scotland, but to some extent also in North Wales, the Lake District, and Ireland, show a distinct vegetation generally known as "arctic-alpine." This name is appropriate because the characteristic species are at home in arctic Europe, and some occur also in the European Alps. Arctic-alpine vegetation is found most richly developed and forming varied plant communities on the mountains formed of basic rocks. The acidic summits, ledges and screes show a few species, but these mountains are generally mainly covered with moor or moss, except where there is bare rock exposed.

All the arctic-alpine *vegetation* lies above the zone of former woodland, though individual *species* may be carried down streams, appearing at lower levels ; and some, especially on the Atlantic coast of Ireland, occur at sea-level.

The lowest zone of this vegetation is the so-called arctic-alpine grassland, represented mainly by an association dominated by the viviparous form of the sheep's fescue (*Festuca ovina* forma *vivipara*) and the alpine lady's mantle (*Alchemilla alpina*), with a number of other characteristic species associated. Above the slopes which bear this type of grassland we come to the sheltered rock faces, ledges and stream-sides which form the habitats of the greater number of the characteristic arctic-alpine species. The individual communities formed by these are generally small, owing to the very uneven nature of the ground, and the study of this varied vegetation is not sufficiently advanced to allow of any useful summary. Finally, we have the summit plateaux

with surface composed of loose rocks ("mountain top detritus"), which are a very regular feature of the higher British mountains; and this is occupied by a sparse vegetation of which the shaggy moss *Rhacomitrium lanuginosum* is the most prominent member.

Maritime Vegetation.

The last types of vegetation we have to mention are the maritime communities developed on the seacoast, whose habitats are determined by "maritime factors." On the one hand we have the vegetation of blown sea sand forming the well-known coastal dunes (and close to this we may put the closely allied though distinct vegetation of shingle beaches): on the other the very different vegetation of the mud flats (so-called salt marshes), which are covered by the higher tides.

The dominant factor of the sand dunes is the loose, moving sand, not the sea salt, for we find communities of very similar type on blown sand on the shores of freshwater lakes, for instance Lake Michigan in North America. The salt marsh plants, on the contrary, are primarily determined by their periodic immersion in salt water, and by the fact that they are rooted in soil where the water is always more or less salt. These *halophytes* have a peculiar economy, and practically all have more or less succulent leaves.

Dune Succession.—The sandy seashore in front of the dunes, which is wetted only by the highest spring tides, is inhabited (where wave erosion is not too great) by a characteristic open community, of which the sea rocket (*Cakile maritima*), the saltwort (*Salsola kali*), the sea sandwort (*Arenaria peploides*), species of orache (*Atriplex*) and the sea couch grass (*Agropyrum junceum*) are the most prominent members. All of these withstand a certain amount of immersion in salt water, showing a corresponding tendency to succulence; and all (the last named especially, owing to its habit of growth) arrest the dry sand blown on to them and form low sand hills or dunes

through which the plants grow up. The low dunes formed by *Agropyrum junceum* may eventually reach a height out of reach of the spring tides, and this species thus comes to dominate an independent community.

The marram grass (*Ammophila arenaria*) cannot stand prolonged immersion in sea water, but its seedlings freely colonise the sand just out of reach of the highest tides. The plants have the same marked power of pushing up when covered with sand as *Agropyrum junceum*, but they grow much more extensively, so that they form much higher dunes, which they bind and consolidate by the ramifications of their rhizomes and roots. Thus the motion of the surface sand particles is checked, and after a time other species, which cannot colonise moving sand, establish themselves between the plants of the marram. Some of these species are practically confined to sand dunes, but most of them are plants also found in inland habitats. It is to be noted that, contrary to a common impression, the sand of dunes below the air-dried surface is constantly moist.

Eventually the surface of the dune becomes covered with a continuous carpet of vegetation, in which certain lichens and mosses which flourish in the damp sea air, but can withstand periods of drought, are usually prominent. Various grasses also enter, and often largely dominate, the fixed dune surface. Old grass-covered dunes may form a poor pasture, and are often used as rabbit warrens. Scrub is frequently developed upon them. The sea buckthorn (*Hippophaë rhamnoides*) is a characteristic native shrub of some of the east coast dunes, and is very often planted. It is not found wild inland in Great Britain, though it grows abundantly on alluvial gravels in other parts of Europe. Typical heath is developed on some British dunes. Climax forest develops on old dunes in many parts of the world, but not in the poorly wooded British Isles, probably because seed is not available in sufficient quantity, perhaps because the very easily leached soil quickly becomes too acid. Various

trees however (notably species of pine), are successfully planted on dune soil.

Shingle Beach Vegetation.—Shingle beach vegetation has considerable affinity with that of dunes, many species occurring on both. The smaller shingle is often much mixed with sand, so that the habitats are similar. Shingle is piled above the ordinary high-water level of spring tides by exceptional tides, and on a well-developed shingle beach there is generally a distinct "storm-crest" marking the last tide effective in this piling up process. It is on the relatively immobile shingle beyond this crest that vegetation carried down the landward side by the overwash establishes itself, most luxuriantly and characteristically on shingle "spits," rather than on beaches which are formed on the edge of the coast and are continuous with the land along their whole length. The plants of shingle beaches are largely derived from and are dependent on the humus of sea drift carried down among the stones.

The vegetation of shingle beaches which are not sandy is characterised by various species of lichens which cover the surface of the stones, and by societies of certain species of flowering plants, among which the sea pea (*Lathyrus maritimus*), the dock (*Rumex trigranulatus*), the sea campion (*Silene maritima*), the horned poppy (*Glaucium luteum*)—the last two also on fixed sand dunes—the purple herb-robert (*Geranium purpureum*), and varieties of the red fescue (*Festuca rubra*) are the leading species. On old shingle beaches, removed from the direct influence of the sea, an inland vegetation develops, and very often a scrub.

Salt Marsh Vegetation.—Salt marshes, as already mentioned, bear a characteristic halophilous vegetation in which practically all the species are peculiar to this habitat. The mud (or sand) covered by every tide is too mobile for plant colonisation: it is only the stretches which lie above the high neap tides that are ordinarily covered with vegetation. The "sea grass" (*Zostera*), however, which is well

adapted to live submerged for most of its life, is frequently found occupying the flats covered by the neaps, where the race of the tide is not too strong. The glasswort or marsh samphire (*Salicornia herbacea*) is the pioneer on the mud flats,[1] the surface of the mud being often prepared for it by the green alga *Rhizoclonium*. The glasswort is followed by the maritime grass *Glyceria* (sometimes called *Atropis* or *Sclerochloa*) *maritima*. The course of the succession is now very variable according to local conditions, but taken as a whole a mixed vegetation (the general salt marsh community) appears on the flats covered by most of the springs. In this the sea aster (*Aster tripolium*), sea plantain (*Plantago maritima*), sea arrow grass (*Triglochin maritimum*), sea lavender (*Statice limonium*), sea spurrey (*Spergularia marginata*), sea blite (*Suæda maritima*), are general constituents.

The salt flats covered only by the higher spring tides bear a turf which is a direct result of the closing and consolidation of the general salt marsh community. This is nearly always grazed and is good sheep and cattle pasture, or saltings, the French *prés salées*. The turf is composed of *Glyceria maritima*, or a form of *Festuca rubra*, with *Suæda maritima*, *Armeria vulgaris*, *Statice limonium*, etc. Locally on the south and east coasts of England the shrubby *Suæda fruticosa* occupies a rather special habitat on the edge of shingle beach where this overlies salt marsh. Other species which occur in the various special habitats at the higher levels of the salt marsh are the sea purslane (*Obione portulacoides*, the sea wormwood (*Artemisia maritima*) the stag's horn plantain (*Plantago coronopus*), etc., and locally various species of sea lavender (*Statice*).

The highest levels of the salt marsh, only reached by the very highest spring tides—perhaps only by a few tides twice a year—is often marked by a belt of the sea rush *Juncus maritimus*, and at the same level we find especially such plants as *Glaux maritima*, *Agropyrum pungens*, and some-

[1] Several closely allied annual species of *Salicornia* may be represented.

times other species, such as *Oenanthe lachenalii*, which is also found in brackish marshes. These species do not show the characteristic structural features of halophytes to nearly so great a degree as those occurring at lower levels; mixed with them are ordinary land species, which will tolerate small amounts of salt in the soil.

When the tide is effectively kept out of a salt marsh area and there is adequate drainage by ditches and sluices, the salt is rapidly washed out of the soil and non-halophilous species colonise the area. Excellent pastureland, which can be converted into arable, is regularly formed in this way. There is no good evidence that salt marsh can develop by the mere accumulation of silt or humus, without human assistance, into a non-maritime vegetation.

We have not aimed in this chapter at giving more than the briefest outline of the nature and relationships of the chief types of British vegetation. We have necessarily left out of account many plant communities of small extent, such for instance as those of sea cliffs; and also the "artificial" habitats provided by quarries, spoil heaps, roadways and waste places of every description, which are of very diverse rank and status. It was explained in Chapter II that human activity is constantly providing the most varied new habitats, and these become occupied by communities of plants which may be temporary and casual, but may be closely adjusted to their environment, as in all old communities characteristic of habitats of long standing, whether natural or due to human agency. The species of temporary habitats are thus derived from the most various sources, and include weeds and casuals together with certain members of old-established communities which are able to colonise them. For these reasons they provide excellent material for close ecological study.

PART III

METHODS OF STUDYING VEGETATION

CHAPTER VI

SCOPE AND AIMS OF ECOLOGICAL WORK

BEFORE passing to the actual methods of work, it is well to consider the aims the student should keep in view in undertaking ecological investigation. There is no reason whatever why the work of every intelligent and careful student should not add to the general knowledge as well as to his own, for there are still a vast number of things about our common vegetation that we do not know, many of them not at all recondite. But if the work is to have this result it is essential that the student should know exactly what he is aiming at, and that he should be prepared, if necessary, to revise his aims as the research proceeds.

Every kind of scientific investigation has two stages—the descriptive and the analytical. We must first know clearly what the phenomena are—the things or processes we propose to investigate; and thus we must carefully observe and accurately record before we can proceed to find out how they come about. It is the fashion in some quarters to deride "descriptive science," to deny that it is true science at all; but such derision is not in the least justified. Unintelligent description of badly selected things is worthless, but intelligent description of the right things, undertaken in the right way and with a definite end in view, is not only valuable, it is indispensable to the progress of science.

We should never be content with mere description if it is possible to go on to an investigation of causation—of *how things come to happen in the way they do*—for that is the ultimate aim of science. Nor is it at all necessary or desirable to divide our work sharply into two parts, descriptive and analytical, and to finish one before we begin the other. The careful description of some sets of phenomena, for instance of some natural processes, especially if it is quantitative, at once enables us to understand their causes, which we could never have done without it. And even if the problem cannot be solved at once, a careful description will enable us to state it more clearly and precisely, so that we can proceed to the necessary analysis or to experiments in the field or the laboratory.

The scientific description of British plant communities is very far from complete. In one sense, of course, it can never be complete, but there is a good deal that wants doing to improve, and to fill gaps in, the existing general descriptions. A good beginning was made during the first decade of the present century, and the results were recorded in *Types of British Vegetation*, published in 1911. Since that time, for various reasons, the work that has been done has been less systematic, and more largely devoted to special problems. The communities that have been distinguished require testing over a wider extent of country than has been actually investigated, in order that the statements made concerning them may be confirmed or modified.

The method of *primary survey* (see Chapter VII), on which the general classification of associations mainly rests, was to choose a stretch of country and then distinguish and map the communities that could be conveniently represented on the scale of 1 inch to the mile by means of different colours, modified by stippling and hatching. The first surveyors had, of course, everything to learn. They had to determine on the kinds of vegetation which they would select for representation; and later surveyors, besides finding new

types in new areas, did not always agree that the original ones were rightly chosen. Towards the end of what we may call "the period of primary survey," the British Vegetation Committee, a small organisation of those actively interested in this work, made an attempt to standardise the colours and symbols used. The scheme drawn up was, however, never published, partly because of the increasing difficulty of securing publication of the coloured primary survey maps, partly because it was felt by some that standardisation was rather premature.

The usefulness of primary survey is certainly not exhausted. It is quite possible to avoid the expense of producing coloured maps by substituting representation in black and white (see Fig. 1, p. 72), though this is not quite so satisfactory as representation in colours. There is no better training in extensive study of vegetation than carrying through the primary survey of a suitable area, because a considerable number of different types are encountered in the course of the work, and the relations of these have to be closely studied in order to represent them properly on a map. There is a good deal to be said for the constant direction of effort to the making of a good map, though this is not of course to be regarded as the ultimate goal of any ecological work, which is the understanding of the vegetation studied. But the making of a map focusses effort and compels the student to make up his mind about the status of the vegetation mapped. As we shall see in the next chapter, it is often necessary to "interpret" vegetation, since it is not possible on a small scale to record every plant population exactly as it is, and the necessity of such interpretation is in itself a valuable training.

There is, however, another method of extensive work, which leads perhaps to a deeper understanding of individual plant communities. This may be called the *monographic method*, and consists in taking a single well-defined plant community, a consociation or an association, such for instance as the

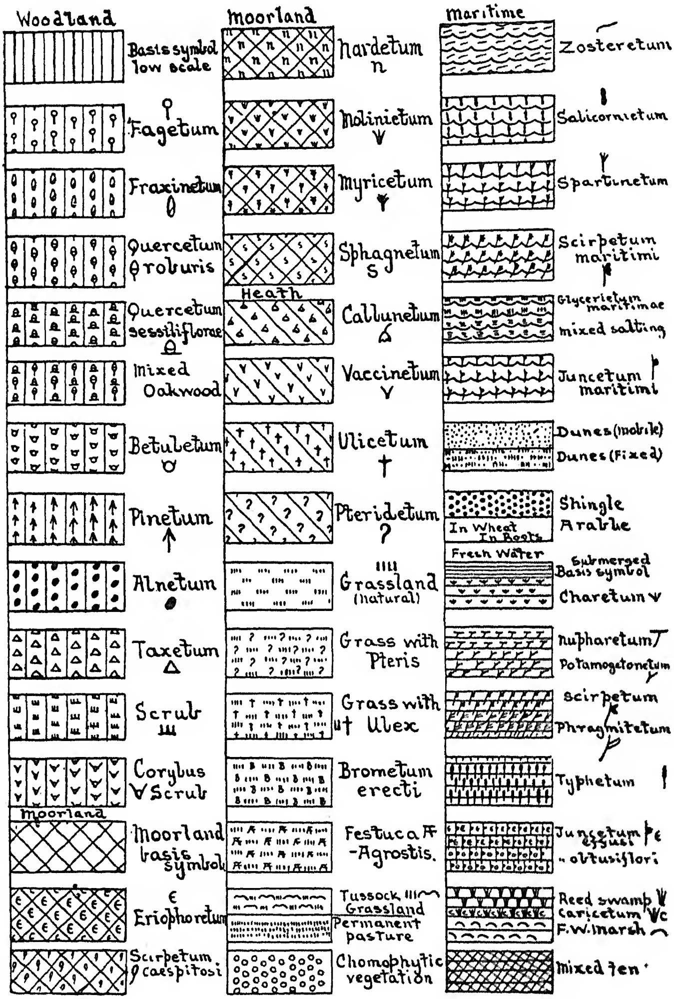


FIG. 1.—Draft scheme prepared by a Committee of Council of the British Ecological Society, under the chairmanship of Dr. E. J. Salisbury, for the representation of British Vegetation in black and white. The scale of the symbols should be varied in accordance with the scale of the map. In general only the " basis

oakwood, the heath or the reed swamp, and following it wherever it is to be found, studying the variations of its composition and structure, its relations to other communities into which it passes by gradual transitions, and its dependence upon habitat factors, climatic, edaphic and biotic. A study of this sort, properly carried out, even over a comparatively small area of country (though it is certainly desirable to extend the study beyond the limits of size of a region convenient for primary survey), will give a deeper insight into the community selected than could be gained from the attention possible during a general survey, and will surely contribute most usefully to knowledge.

Both the primary survey and the monographic methods are essentially *extensive*, carried on over a wide area of country, primarily by the methods of observation and comparison. On the other hand, what may be called *intensive* work is concerned rather with detailed investigation of particular problems in *one* spot. These problems are endless, and may be pursued to any length that the inclination, abilities, opportunities and means at the disposal of the student may dictate. Among them may be mentioned such things as the whole set of problems centring round the *multiplication* and *dispersal* of individual species: the amount of fertile seed a given species produces under different conditions, the actual means by which the species spreads, the rate of spread; the conditions under which germination can occur and establishment of the seedlings take place. Closely linked with these problems are those concerned with *competition* between individual plants, either of the same or of different species: the success or failure of one or the other of two competing species and the actual means thereof; for instance, root competition or over-

symbol," representing the general type of vegetation, should be employed in small scale maps. The other symbols, representing consociation dominants, can be added wherever the scale permits of the separation of consociations. (Reprinted from the *Journal of Ecology*, 8, p. 61, 1920.)

shadowing; the effect upon the result of different conditions of the habitat, for instance moisture or reaction of the soil. Then there are the one-sided or mutual *benefits* which plants may confer upon one another, for instance the protection afforded by a larger plant by way of shelter from desiccation. or by a spinose plant in keeping off the attacks of browsing animals; and again the preparation of the soil by the formation of humus from the decaying parts of one plant for the establishment of others, and so on. On the solution of numberless problems of this nature depends the detailed understanding of every case of natural *succession* (see Chapter IV), and some of these, at least, can be studied with every prospect of success by anyone who lives in the country and has time at his disposal.

In working at such problems it is important to employ *experiment* as well as observation, wherever possible. This can be done in the field wherever there is little or no risk of disturbance. It must be admitted that the likelihood of disturbance is a serious drawback to the setting up of experiments on vegetation in the English country-side. It is often possible, however, to obtain the toleration or even the interest of landowner, farmer or keeper, and thus help to secure the safety of field experiments. And some experiments which do not require apparatus of any sort are quite inconspicuous.

The importance of field experiments in ecology cannot be overestimated. It must not be supposed that experiments necessarily imply instruments or apparatus, elaborate or simple. The experimental method simply means the observation of processes under controlled conditions. The nature and extent of the control necessary are of course infinitely various according to the problem under investigation. For instance the fencing of a small area against rabbits,[1] the cutting of small narrow trenches to divert the water supply which ordinarily flows down a slope in a region

[1] (**33**) Farrow II, 1916; (**45**) Tansley, 1922; (**57**) Watt, Part I, 1923.

of heavy rainfall,[1] the supply of extra water to vegetation growing on dry soil[2]—all these are field experiments which have given valuable results. Such experiments are essential for the solution of many ecological problems, and moderate ingenuity will suggest an indefinite number of means of testing the effects of the different factors at work upon vegetation.

Many ecological processes can be conveniently studied in a garden, but it must of course be recognised that the conditions in a garden are very different in many respects from those of natural vegetation, and caution is required in making inferences from one to the other. With this proviso a great deal of information can be obtained from garden experiments. Natural conditions can sometimes be closely imitated by growing plants in competition in boxes filled with the natural soil of their habitats. But such work can never replace observation and experiment in the field.

Something may be said here about quantitative methods. The determination of exact quantitative results from which quantitative laws can be formulated is a well-established method of science. Broadly, we may say that in proportion to the advance of a branch of science its methods become quantitative. This is as true of biology in general and of ecology in particular as of other branches of science. But neither biology in general nor ecology in particular can as yet be treated wholly or even mainly by quantitative methods, though these should of course be applied wherever they are in place. Quantitative data are not *necessarily* of any value, and we must never make a fetish of them. To be of value for making inferences and ultimately formulating "laws" they must have some kind of *general validity*, i.e. they must either form parts of a general descriptive "picture," or they must be of such a kind that they can be causally related to one another. Isolated data or sets of data which do not fit into a "picture" and cannot be causally related are valueless, or nearly valueless. This is

[1] (30) Jeffreys III, 1917. [2] (33) Farrow IV, 1917.

equally true of enumerations of species and frequencies, and of quantitative records of the factors of the habitat, such as soil analyses, evaporimeter readings, light records, and so on. The mere taking of an instrument into the field and making readings, just as the mere recording of the number of individuals of a species in a given area, is not a virtue in itself and is no guarantee of scientific results. If we would discover causation there must always be a definite object in view, a definite problem to be solved, and observations and records and experiments must always be directed towards solving it. All this may seem very obvious, but it is not infrequently forgotten.

On the other hand, intelligent qualitative observation of the constitution and relationships of plant communities, sometimes at once enables us to recognise causes, or at least clearly to state problems for solution. In so far as qualitative observation contributes to a picture of the vegetation of a country or region, it is essential in the first descriptive stage of investigation; a few quantitative data may be added by way of closer characterisation. But it is of little use to multiply these last indefinitely until specific problems arise and can be clearly stated and deliberately attacked.

In attempting to attack a specific problem the best mode of approach should first be carefully thought out. Ecological problems are often complex, and it may soon appear that the method of attack first chosen is not giving the desired results. One problem leads to another, and it may be necessary to abandon the first till the second has been worked out. The attempt to solve the second may, in its turn, show that a third must first be attacked, and a successful solution of that may cause the first to disappear altogether. For instance, suppose we are trying to explain the puzzling distribution of two or more plant communities over a certain area of ground. At first it may be thought that the undoubted variations in texture and chemical constitution of the soil are responsible. But soil analyses

nay show that none of these variations can be connected lirectly with the differences of vegetation. There may ippear evidence that these differences correspond, to some extent, with the moisture of the soil, though the communities nhabiting, on the whole, the drier and damper areas espectively are apparently quite capable of growing on either. This suggests a difference in the incidence of competition between the plants of the two soils, and the difference n competition may finally turn out to be determined by the ittacks of animals which avoid, for instance, very wet ground, and bear more hardly on one of the communities which they prefer, thus handicapping it in its struggle with the other, except on the wet ground where it is not so heavily ittacked. The original problem, the correlation with soil constitution, has vanished, and the question of moisture has become subordinate, in determining the observed distribution, to that of competition as affected by animal attack, which thus turns out to be the main cause of the distribution observed. Such a case as this (cf. Farrow, Breckland II, III, IV, and V, see list, p. 218) clearly brings out the necessity of keeping an open mind, and not persisting in a line of attack which is not giving good results.

Also the student should never allow himself to become enslaved by his *methods*. The method which seems most suitable should be carefully thought out beforehand, and strictly adhered to until it is thoroughly tested. But it should be modified or abandoned directly it proves unsatisfactory, and a better one can be substituted. Never adhere to routine for the sake of routine. This warning applies particularly to listing, charting and mapping methods (see Chapters VII and VIII). A great deal of valuable time may be wasted, for instance, by adhering to laboriously accurate methods which are giving little information likely to be of value. This is not to say that detailed charting, for instance, in which the position of every individual plant is shown, is not sometimes of essential value. It all depends on the particular object in view.

CHAPTER VII

EXTENSIVE STUDIES—RECONNAISSANCE AND PRIMARY SURVEY

IT was remarked in the last chapter that an extensive study or survey of a large tract of country—primary survey, as it is called—forms a good preliminary to intensive work. Such a survey gives a general knowledge of the types of vegetation and the conditions in which they occur, and enables the student to choose areas or communities for more detailed study with skill and judgment. This advantage is quite apart from the aim of making accurate maps of the vegetation of considerable areas, which is a legitimate and useful end in itself.

RECONNAISSANCE.

In the same way the even more cursory work known as *reconnaissance* is a desirable preliminary to primary survey. In reconnaissance the country is rapidly traversed, the salient features of the vegetation noted and samples here and there are listed, so that the student gets a general idea of what the field is like. Primary survey is a good preliminary, though by no means an essential preliminary, to intensive detailed work, but some sort of previous reconnaissance is practically necessary before primary survey is undertaken.

The first thing to do before starting on reconnaissance is to obtain a good contoured topographical map of the district to be reconnoitred, such as Bartholomew's excellent "layer contour" maps on the scale of half an inch to a mile

(1 : 126,720).[1] or the maps of the Ordnance Survey on the scale of 1 inch to a mile (1 : 63,360),[2] and also if possible maps showing the surface geology (which is usually all that matters to the ecologist), for instance the " drift maps " of the Geological Survey on the same scale, if these are available.[3] From the topographical and geological maps the general nature of the ground and of the soil, the situations of woodland and " wasteland," can be seen in a general way, and the best routes chosen. A bicycle (or motor car) is a very useful help in working the area quickly, though in the remoter and more sparsely populated districts, where there are few roads, it is often necessary to leave such aids to travel and traverse the country on foot.

Each well-marked type of natural or semi-natural vegetation met with should be rapidly examined, and the dominant and abundant species, as well as any peculiar or striking species, recorded in the notebook. It is best to keep a special notebook for reconnaissance work. At the same time the principal agricultural crops should be recorded. It is convenient and useful to record *on the map itself* (e.g. Bartholomew's half-inch or the large sheet folding map of the 1-inch Ordnance Survey) the general type of natural vegetation, plantation, arable or pasture land. This can be done by means of symbols, preferably letters denoting the generic names of the dominants of natural vegetation, or in the case of crops the English names. But the method employed must be left to the judgment and convenience of the individual.

A small portable pressing-case for taking home unknown or doubtful plants, a snapshot camera, and a tightly stoppered bottle of dilute hydrochloric acid[4] for roughly

[1] Price 3s. per sheet, mounted in sections, 4s.

[2] Price of " Popular Edition," each sheet of 27 inches × 18 inches, folding for the pocket, 2s. 6d., mounted in sections, 3s. 6d.

[3] Unfortunately, " drift maps " of considerable parts of the British Isles have not yet been published.

[4] E.g. 20 per cent. Note that hydrochloric acid destroys cotton and linen fabrics, but not those made of pure wool. It is almost

testing the amount of "lime" (calcium carbonate) in the soil, are useful accessories; but the map, notebook, sharp eyes and a wide-awake mind are the only essentials.

In reconnaissance proper it is important to keep to the *aim* of reconnaissance, i.e. to get a *general* idea of the country and its vegetation, and not to allow the interest to become fixed on particular communities. Primary survey work cannot be done properly on reconnaissance, and time is spent with no satisfactory result if the student lingers too long over one community. At the same time this warning must be interpreted with common sense, for instance if something particularly interesting is met with, and there is likely to be no opportunity of revisiting the spot.

It will be obvious to the reader that successful reconnaissance work presupposes at least a moderate knowledge of species and of soils. For the rest it can be carried out with increasing rapidity and increasingly trustworthy results as experience accumulates; but the beginner, if he knows his plants and has some knowledge of rocks and the soils they produce, can obtain useful results.

No attempt should be made in reconnaissance to cover every square mile of the country: that is the business of primary survey. The aim is only a general result based on observation along well-chosen routes. The time necessary to carry out a fairly complete reconnaissance varies greatly with the type of country. Regions with very uniform vegetation, if they are reasonably accessible, occupy far less time than greatly diversified regions, which are always time-consuming in extensive work. In steep, hilly country it is often possible, with a certain amount of experience,

impossible to avoid occasional drops getting on the outside of the bottle, and from there to the clothes. It is useful to have a rough subjective scale of reactions of soil to hydrochloric acid, e.g. L_0 no bubbles, L_1 few isolated bubbles, L_2 slight general effervescence, L_3 moderate, L_4 strong, L_5 violent. It should be remembered that the surface inch or two of the soil often contains practically no lime, owing to leaching and humus formation, while slightly deeper layers, in which some of the plants are rooted, may contain a considerable percentage.

to identify, *for reconnaissance purposes only*, the type of vegetation on an opposite slope from its general appearance at a distance, and in this way much time may be saved. Similarly, good reconnaissance may sometimes be done from the windows of a slowly moving train. It is unnecessary to say that such observation is no *substitute* for actual survey, since many detailed features and local variations will naturally be missed altogether.

Primary Survey.

This name is applied to the general method adopted by the first ecologists who began to study British vegetation systematically at the end of the nineteenth century. It was based on the methods of Professor Flahault of Montpellier, and consisted essentially of recognising and describing the larger vegetation units (mainly associations and what we now call consociations), making lists of their floristic composition, studying their relationships and the general nature of their habitats, and recording their distribution in colours on topographical maps of the scale of half an inch or, latterly, of 1 inch to the mile.

The making of the map was an end in itself, though the map might also be regarded as an illustration of the descriptive paper which it accompanied. Such maps, on a uniform scale, and with a uniform system of colouring, have been rightly compared with the series of coloured geological maps issued by the Geological Survey. A series complete for the whole country would present a graphic record of the distribution, not only of the main types of natural and semi-natural vegetation, but also of the principal kinds of cultivated land. This last has to be treated somewhat differently from the native vegetation, since it is impossible to map all the actual crops, if only because they change from year to year in accordance with the system of crop rotation employed. The earliest surveyors in Scotland and the North of England distin-

guished "upland cultivation with oats" from "lowland cultivation with wheat" by different shades of yellow, and later surveyors introduced additional types. The shade of yellow represented, however, not only the land actually under wheat, but the whole area where wheat *could*, presumably, be grown. Eventually it was proposed, by hatching green upon yellow, to indicate the approximate percentage of permanent pasture in the farm land, and thus to distinguish, for instance, the Midlands and West of England, where pasture largely preponderates, from East Anglia, where much the greater area is arable. This proposal, certainly a good one, was never carried out because the publication of the primary survey maps came to an end. Further differentiation of cultivated land could and should be made in mapping areas in which it bulks largely.

The absence of any hope of completing a series for the whole country within any reasonable period, partly because of the expense of publication and partly because the interest of ecologists became more concentrated on special problems, together with the facts that the published maps are on different scales, employ to some extent different colours, and appeared in forms not readily accessible to the public, rather seriously detract from their general usefulness. The primary surveyors, however, did yeoman service to our knowledge of British vegetation. They began the modern systematic study of vegetation in this country, they formed the first organisation for its promotion, and they provided the essential basis for the general treatment published in *Types of British Vegetation.* It may be possible in the future to revive the aim of a complete series of primary survey maps of the vegetation on a uniform scheme, if interest in this particular type of work should again be aroused in adequate measure. In the opinion of the author there is no better training in the practical study of vegetation than the work of primary survey, just as there is no better training in field geology than geological mapping.

The area chosen by the individual surveyor for primary survey must generally be determined by its accessibility, Very frequently, of course, it is the area in which the surveyor lives, for much time has necessarily to be spent in the field. Sometimes it may be possible to undertake the survey of an area in which the surveyor spends successive summer holidays. Few people have the means and leisure necessary to make extended visits to remote regions, however interesting they may be. If a choice is available it will clearly fall on a region with much natural and semi-natural vegetation which is striking, diversified and generally interesting; unless indeed the surveyor's interests are predominantly agricultural, when he may choose a region mainly from that point of view. On the whole it is most convenient and useful to take an area coincident with one or more sheets of the 1-inch Ordnance map in preference to a "natural" region bounded for instance by the limits of a geological formation or a river basin. This course involves no waste of space in presentation of the results, and gives more varied data on an equal surface of land. It has the further advantage that the finished sheets will eventually fit together in a complete series for the whole country. An area coinciding with one "large sheet" Ordnance map 27 inches by 28 inches will be amply big enough to begin with. It is always a mistake "to bite off more than you can chew."

Field Equipment.

Field Maps.—These should be the 1-inch and 6-inch Ordnance Survey sheets of the selected area. Two copies of the 1-inch sheet will be required—one unmounted and uncoloured, the other dissected, mounted and folding for the pocket. These maps can be bought in both forms direct from the Ordnance Survey Office, Southampton, from Stanford, of Long Acre, London, or from a local agent. The sheets of the Outline Edition (1s. 6d. each) measure 18 inches by 12 inches, and the unmounted copy should be

cut up into eight parts, each measuring 4½ inches by 6 inches, and mounted on cards of the same size.[1] On the backs of the cards should be written the number of the sheet and the number of the section (1–8), and there will also be space for any desirable explanation of the symbols used on the face of the map, and for any necessary general notes referring to the section. This plan is very convenient because each mounted section of the map can be conveniently held in the hand and worked on separately, and several sections can be carried in a canvas or waterproof pocket made for the purpose and measuring say 6½ inches by 5 inches.

For uniform country like mountain and moorland, and for purely agricultural country the 1-inch map will often suffice, but in varied country where the vegetation changes frequently within a short distance, or wherever details require to be mapped for proper elucidation, 6-inch field maps (1 : 10,560) are necessary. The quarter sheets of these (18 inches by 12 inches, price 1s. 6d. each) can be cut into eight sections and mounted on cards of the same size (4½ inches by 6 inches). When no detailed work on the map is required, it is unnecessary to cut them up, and they can be carried whole in a folding leather case. There is no need to buy these 6-inch maps unless and until they are individually required. The new 6-inch maps are being published in full sheets (36 inches by 24 inches), price 5s. each, superseding the quarter sheets.

Notebooks and Note-taking in the Field.—Any convenient pocket notebook may be used.[2] The individual surveyor will have his own preferences in regard to the system on which the notes are taken. All that need be said here is that systems of note-taking, as of other things, are very

[1] Cards of this size are also useful for mounting blank quadrat charts (see p. 109), and it is convenient to cut or have cut a considerable supply.

[2] Some observers recommend carbon duplicate notebooks, so that they may leave the duplicate at home, and avoid the possibility of loss of the whole season's notes.

useful so long as they are not slavishly followed when they become unsuitable. The great advantage of following a well-thought-out system is that it tends to completeness of record and ease of reference. One of the commonest experiences of a surveyor of vegetation—and indeed of any worker whose business it is to make records of observations that he cannot immediately repeat at will—is to find, when he comes to write up and think about his notes, that he has omitted to make or to record observations which turn out to be important or even essential for his purpose.[1] A good system will partly prevent such omissions, provided the system is constantly modified and improved in the light of increasing experience. But no system, of course, can be a substitute for the activity of an alert and imaginative mind.

It is always essential to make notes *on the spot* of every fact that is or may be worth recording, with scrupulous emphasis on any fact which runs counter or appears to run counter to a previous conclusion or preconceived opinion. And the records of facts should be accompanied by, but clearly distinguished from, any hypotheses or conjectures that occur on the spot, or later in the day, while the observations are fresh in the mind. The importance of full systematic note-taking and constant consultation and revision cannot be over-emphasised.

Remaining Field Equipment.—Map and notebook are the only *essentials* in primary survey, that is to say these are always required, and good primary survey work can on many occasions be done with these alone. But of course no primary survey can be satisfactorily carried through without the frequent use of other articles of equipment. The things that may be necessary or useful are, however, too numerous to carry conveniently on every field excursion,

[1] Wet days or " off days " should be used for revising notes, making draft descriptions of the vegetation seen, etc. Gaps in observation thus revealed can be made good at a second visit to the spot.

and a selection must usually be made between them. It is a mistake for the average individual to load himself up too heavily with varied impedimenta, because this leads to fatigue and often to inferior quality of work. Few people can keep an alert mind when they are tired with carrying a heavy weight. Further, the presence of equipment for too many different kinds of work tends to distract the attention from the general records and problems, for dealing with which it is necessary to keep the mind free for direct observations on the vegetation.

For these reasons it is usually desirable to make observation, recording on the sections of the field map, listing and note-taking, the main objects of the first working over of a section of country; leaving soil testing, or collection of soil samples, light records, photography and other detailed work for a second visit, on which, of course, the first records can be checked and if necessary revised.

It is always well to carry a *pocket flora*, such as *The Botanists' Pocket Book* (Bell, 5s.), for determining doubtful species on the spot. A good *pocket lens* should always be carried by every botanist. The beginner who does not know his species well (and sometimes the more advanced student) will have to take home with him specimens for determination. For this purpose a small, light, *portable pressing-case* that can be slung over the shoulder, *and easily opened without unslinging*, is more compact, and often more convenient than a vasculum.

A tightly stoppered bottle of dilute *hydrochloric acid* (see p. 79, footnote 4) is frequently very useful, though it is not wanted on siliceous soils which are known to contain minimal amounts of calcium carbonate. A *measuring rule* (e.g. a carpenter's folding foot-rule) is often useful, and so is a *photographic actinometer* for light records (see p. 135). All the above, together with notebook and sections of maps, can be carried easily enough in a light haversack or in roomy pockets without encumbering the surveyor.

A *camera*, on the other hand, *tins for soil samples*, and a *strong trowel* for examination of root systems and for collecting soil samples, are relatively bulky, and it is these which are often better left for separate excursions. Details concerning photography and the study of soils will be found in the Appendix (pp. 204–15) and in Chapters XI and XII. Here it need only be said that a folding roll-film camera may be used by the primary surveyor for snapshots of general views of brightly lighted vegetation,[1] and a few small (i.e. 2- and 4-ounce) tobacco tins are often handy for small soil samples or small plants which it is desired to take home fresh.

Method of Work in the Field.—In planning a day's primary survey it is important, if time is to be economised, that a fairly close idea of how much ground can be usefully covered should be formed beforehand in order that the route may be appropriately planned. In the first place, it must be borne in mind that the aim of primary survey is to record, and as far as possible to understand, the vegetation of the whole area to be mapped. All the ground must be visited at least once. This does not of course mean that every square yard or even every acre must be examined. At first, before experience of the plant communities to be found in the area under survey has been gained, a great deal more time will have to be spent on recording and listing the species met with than will be necessary later on.

On approaching a particular community it is advisable for the beginner to concentrate attention on a small area which appears to be typical, and to lay down a quadrat (see p. 108) which can be examined in detail, the species present identified, and a short description of the vegetation written. A second and a third quadrat may then be laid

[1] Really good photography of vegetation is one of the most difficult branches of the art. Experience, of course, teaches what will photograph well and what will not. Broadly speaking, general views with sufficient contrast in *bright* diffuse light are the subjects most likely to be successful with a snapshot camera. The air should be clear and dry, not misty. (See pp. 204 ff. for further details.)

down in other places, and the same procedure followed. In this way an accurate idea of the species present and of the structure of the vegetation is gradually built up.

On the preliminary reconnaissance a general idea of the broad features of the vegetation will have been formed. One of the first tasks of the survey proper is to determine what plant communities are to be recognised for mapping purposes. These will be primarily associations and consociations of the natural and semi-natural vegetation. Typical samples of these must be thoroughly examined, their species listed and the main features of their structure recorded. The consociations must then be recorded on the sections of the field map by symbols—the initial letter of the generic name of the dominant is the best—the associations by collections of initials, or other convenient symbols. Boundaries between different consociations or associations must also be drawn, and where there are zones of considerable width, transitional between two communities, these must be marked. Sometimes all this can be done on the 1-inch map, sometimes the 6-inch map will be required.

Many doubts and difficulties will soon appear, largely caused by the modification and fragmentation of the vegetation through human activity. Areas which present too many and bewildering difficulties of interpretation may be roughly described in the field notebook and then left over until further experience has been gained. This will often automatically clear up the difficulties, and then the doubtful areas can be revisited and included in the map. The ideal of recording the vegetation actually on the ground and nothing else cannot always be strictly adhered to. It is quite impossible to represent on a comparatively small scale, such as 1 inch to a mile, all the actual variations met with, whether caused by local variations of habitat or by human interference. The surveyor will soon discover that he is obliged to group many such variations under one type. One of his first tasks is to decide upon the types he

will choose in the first instance, but these will very likely have to be modified later on. The notebook should of course contain full notes on the variations, and every effort should be made to discover their causes. These should be dealt with as far as possible in the final description of the area surveyed.

To give an example of what is meant. Suppose a woodland of definite type extends over a certain tract of country. Most of it may be in a stable semi-natural condition, for instance standards of a certain species of dominant tree, and coppice composed of certain species of shrubs in fairly constant proportions, with a ground vegetation of similarly uniform characteristics. Clearly that tract of country must be represented as uniform, and marked with the initial of the dominant tree representing the consociation, even though it may include areas of a few acres here and there which actually differ from the type more or less widely. The ground may be wet in some places owing to the water-level being close to the surface, and the typical vegetation of the woodland may here be mixed with or replaced by other species which favour wet soil, though such local societies are much too small to show on the map. If a special study of the woodland is being made, they may of course be shown on the 6-inch map, but in any case they must be recorded in the notes. In some places there may be no standards at all, but only coppice of the same general type as where the standards are present. Other areas may be completely replanted with conifers; if these are large enough, they can be indicated by the appropriate initial on the map. In others, again, the wood may have been cleared or partly cleared and left derelict, or cattle may have been allowed to graze through it, causing considerable modification of the vegetation, such as the entrance of many species alien to the woodland and the disappearance of some woodland species.

The detailed recording and study of such effects scarcely

belongs to primary survey proper, and it is quite legitimate to lump the whole together as belonging to the typical woodland, when it has quite clearly been derived from this by human agency. In process of time, of course, the original woodland may be converted into something totally different, for instance grassland, or it may be ploughed up and turned into arable fields; and then naturally it can no longer be reckoned as belonging to the original woodland. Similar cases are provided by the partial drainage of marshes and bogs, by the heavier pasturing of certain tracts of grassland, and so on. These differential treatments may cause very great differences in the vegetation, but the whole area of marsh or grassland has often to be treated as a unit for primary survey purposes.

A good deal of useful information may be obtained by getting into conversation with woodmen, gamekeepers, farmers or shepherds. It is not advisable to accept all they may say at its face value, but such countrymen can very frequently tell the surveyor things which he could not easily find out for himself. Experience and observation provide a test which makes it possible to sift such information. It is also sometimes possible to get useful data from landowners or their agents or bailiffs about the past treatment of land. Old maps are often very valuable sources of information as to the condition of an area in former times.

Listing of Species.—The making of careful lists of species occurring in the different communities is one of the most important tasks of the primary surveyor, for the actual flora of a plant community is, of course, its essence. It is often not a straightforward matter to make a satisfactory list, because of the modification of the original composition of the community, especially by the entrance of species from outside owing to human interference. Thus one may often find in a coppiced wood a number of species which are not true woodland species, but which enter the wood when it is opened up, either by the agency of wind or because

their fruits or seeds are carried there by traffic.[1] Such species are able to establish themselves in the wood because of the light which reaches the ground owing to the absence of a continuous thick tree canopy such as exists in "high forest." Some are distributed through the coppice, others are confined to rides and pathsides.[2] They may have the most various origins, but many of them belong to the class that are often called "marginal," i.e. they are characteristic of the semi-shade of wood margins, hedge banks, etc. Others may be pasture plants or wayside or arable weeds. Similar cases of the collocation of species of very different origins occur in many other modified habitats.

It is not possible for the beginner to distinguish between such different categories of plants, and the only safe course is to make a complete list of all the species which actually occur within the limits of the community; but it is, of course, necessary to add notes when the habitat is clearly modified.

When a community is definitely stratified, it is best to list the constituents of the different strata separately. In a wood it is very easy to distinguish the strata (see p. 36), but in some communities, particularly in grassland, the stratification may not be very definite, i.e. the plants may vary greatly in height, and some of the species may bridge the space between two successive strata, expanding their basal leaves, for instance, in one stratum, and their upper leaves in a higher one. It is always well to spend some time studying the phenomena of stratification in such a community, for it is an important structural feature of

[1] We still know extraordinarily little of the ways in which most species are actually dispersed from place to place, but such evidence as we do possess tends to show that in a populated country they are very largely carried about in the clothes and on the boots of people, in the mud on cattle and horse hoofs, etc. Men employed in coppicing and felling may carry seeds through a wood in this way. Others never get beyond the paths or rides.

[2] This may be a question of dispersal, but the two habitats are different in more than one way, and practically always bear different species and societies.

the community, and is of great ecological interest, because the actual habitat conditions may differ considerably in the different strata.

Frequency Symbols.—Some index of the frequency of each species recorded should be added to its name. It is usual in British lists to employ the following symbols.[1]

d = dominant	*o* = occasional
a = abundant	*r* = rare
f = frequent	*vr* = very rare.

The letter "l" is prefixed to the symbol when the dominance, abundance or frequency is *local* only: thus la = locally abundant.

The dominant of a society within the association is of course "locally dominant" within the association. Dominance has reference to a given layer only: thus the pedunculate oak (*Quercus robur*) may be dominant in the tree-layer, the hazel (*Corylus avellana*) in the shrub-layer, the primrose (*Primula acaulis*) in the herb-layer, and there may be a moss-layer, in which for instance *Catharinea undulata* or some other species is dominant. When two or more species share the dominance in a given layer, "co-d" (co-dominant) is used, but in some communities there is such a mixture that no species or group of species can be said to be generally dominant. This is particularly the case in transitional communities.

The assignment of frequency symbols such as those mentioned depends of course upon a subjective judgment without a fixed quantitative standard, such as could be obtained for instance by recording the species occurring within each of a large number of small areas of uniform size (say 1 foot in diameter) taken at random. The best method for the numerical determination of frequency is still a matter of controversy, and such methods are not in any

[1] Some botanists use a larger number of symbols than those given, but this course is not recommended, at any rate for the beginner.

case suited for primary survey. The judgment as to whether a species is "frequent" or "occasional" in a given community is easily made after a little practice, and the standard does not in fact vary perceptibly between different workers. It should, however, be clearly realised that it does and must vary with the size of the area listed.

Let us suppose, for example, that an afternoon is spent traversing in different directions a patch of woodland about a mile square with a uniform flora, that the different species are noted as they are encountered, and that the frequency letters are added from time to time, and checked and corrected with further observation. An "abundant" species will be one which is never or hardly ever out of sight, a "frequent" species one which is not abundant in this sense, but nevertheless is constantly being met with, an "occasional" species one which is seen perhaps five to twenty times in the course of the afternoon, while a "rare" species is only seen once or twice. But if now a small area of the wood—say an acre—is thoroughly searched and the species within it noted separately, the species called "rare" in the wood as a whole will probably not be seen at all, even the "occasional" species may not be present in the particular acre, while the species "frequent" in the wood as a whole will fall to the rank of "occasional" or even "rare." If, on the other hand, the frequencies of species in a large number of woods of the same general type are considered, the plants which are "rare" or even absent in a particular wood may be appropriately called "occasional" in a wide stretch of country; if a certain number of specimens occur in most of the woods, the "occasional" plants of the single wood may become "frequent," and so on. Thus these terms have a significance which is strictly relative to the size of the area considered, and this fact must always be remembered in compiling lists. The frequency symbols given are most suitable for the larger areas, and when a general account of such an area is being drawn up the number of listed

examples of a given association in which they occur, as well as their frequencies within such examples, must be taken into consideration.

Seasonal Changes.—In describing and listing an association it is very necessary to remember the seasonal change in vegetation. This is most marked in deciduous woods, where there is a very distinct "prevernal" ground vegetation; several species of which, such as *Adoxa moschatellina, Anemone nemorosa, Scilla nonscripta,* may easily be missed altogether if the wood is visited only in late summer, their leafy shoots often completely disappearing soon after flowering. But it applies to other associations also. The little spring flowering annuals ("ephemerals") of open spots in dry grassland (such as fixed sand dunes, etc.) completely disappear in the summer. Many of the orchids of chalk grassland are not to be found in late summer or autumn. On the other hand, heath, fen and salt marsh vegetation do not reach their full development till after midsummer.

Visits should be paid at as many seasons of the year as possible. If only three visits are possible in the year, these should be in April, June and August; if only two, early May and July for woods; if only one, then it should be in late June for woods and grassland (except that which is cut for hay), July or August for heaths and fenland, August or September for salt marsh. These months are suitable for most of England and Wales; in the north and in Scotland, particularly the east, most of the vegetation is from three weeks to a month later in the average year.

Objects of Primary Survey.—The study that can be given to the different plant associations during primary survey is necessarily rather superficial. The main object is to distinguish, record and characterise the larger communities met with and to note their relations to topography, exposure, soil type and ground water. But special note should be taken of the relations of the different communities to one another, of advance or retreat; and of successional

phenomena in general; modified, as they are nearly everywhere in this country, or even caused, by the effects of human activity, pasturing of various kinds, drainage, felling, burning, etc. It is in the course of observations of these kinds that problems which have to be attacked by more intensive methods of work can be recognised and noted.

The monographic method, in which one plant community, followed over a wide stretch of country, is the centre of interest, can be pursued by methods similar to those of primary survey, but the observations will be more detailed. The habits and behaviour of the dominant and other prominent species of the community will receive special attention, the floristic composition and its variations, the essential features of the habitat and the relationship to other communities will be closely studied.

CHAPTER VIII

INTENSIVE STUDIES—LARGE SCALE CHARTS OF VEGETATION

When we turn from extensive to intensive ecological work, we begin to come to grips with the detailed problems of vegetation, which cannot be solved by extensive work. Primary survey or the monographing on extensive lines of a given type of plant community over a wide area is largely a geographical study, concerned with the distribution and broad features of the larger units of vegetation. To get to the bottom of the structure and development of individual communities, to learn how it is that particular species become dominant or abundant in some places and not in others, to understand the mutual relations of species, the weapons with which they fight, the advantages they may confer on each other, their reactions to different factors of the habitat, the limits of their tolerance of varying conditions, we must concentrate our attention on particular problems and employ the most various means for their solution. In this field of work, most particularly, elasticity of mind, lively imagination and ingenuity in devising methods of attack, are essential, in addition of course to the always indispensable determination and persistence.

In dealing with primary survey one can describe fairly closely the necessary programme of work, but with intensive work it is impossible to do anything of the kind, because the problems are so various and because they often differ according to the community studied, so that no fixed procedure can be laid down. We shall, therefore, describe in turn some of the methods that may be employed in studying

first the vegetation itself and secondly the habitat. The particular methods chosen by the student must depend on the particular vegetation to be studied, and on the particular problems he can formulate in regard to it. Further, it must be remembered that ecological technique is still in an early stage of development, and therefore there is ample room for new methods of work and for improvement and adaptation of existing ones.

Every genuine original worker in science is an explorer, who is continually meeting fresh things and fresh situations, to which he has to adapt his material and mental equipment. This is conspicuously true of our subject, and is one of the greatest attractions of ecology to the student who is at once eager, imaginative and determined. To the lover of prescribed routine methods with the certainty of "safe" results the study of ecology is not to be recommended.

Since this is a book intended for the beginner, methods which involve any considerable special training are not described. If the investigation of certain ecological problems is to be carried far, the use of such methods cannot ultimately be avoided. The keen student who finds them necessary will be willing and able to train himself to use them. Here the emphasis is laid on problems which need only simple methods, and which are often neglected, partly owing to the excessive prominence of the laboratory in modern botany. Comprehension of much of the behaviour of vegetation, which we still grasp very incompletely, depends on the solutions of these simpler problems, which require only the simplest material aids. An essential aid to the investigation and recording of vegetational data, though always to be used with discrimination and forethought, is the making of vegetation charts.

LARGE SCALE CHARTS OF VEGETATION.

Vegetation Charts represent the details of the vegetation of a small area on a large scale, and are constructed *de novo*,

They are to be distinguished from *vegetation maps*, which are either constructed from topographical maps by plotting the broad vegetational features on the topographical map as a basis, as in the coloured maps of the British Primary Survey; or by making a new map by the methods of land survey (see Appendix, p. 199).

It was explained in the last chapter that the making of a vegetation map which forms part of a uniform series that could be extended to cover the whole country can be regarded as an end in itself, apart from the knowledge acquired and the experience and training afforded by the process of making the map. This is not always the case with the vegetation chart, which should not be made for its own sake, but only as a characteristic sample of the detailed structure of a widely distributed typical community, to illustrate some striking distribution of vegetation in relation to habitat, or (and this is the most important use of charts) as a definite aid to the solution of a definite problem.

Many striking distributions are observed from time to time in the field—for instance aggregations of one species around or among individuals of another, the growth of a species or a community only in positions exposed to or protected from the sun or the wind, the regular zonation of vegetation round a pond or lake, or again round a hillock or on the two sides of a ridge. Very often such features can be sufficiently dealt with by descriptive notes alone or rough charts drawn by eye; an accurate chart to scale would not repay the time spent upon it. But in other cases the interest of the distribution and the accuracy with which it follows the habitat conditions seem to demand an exact chart, and the close observation required for this purpose may reveal the existence of other factors not at first suspected, or may show that the correlation with habitat, which seemed obvious, breaks down. The judgment required for a correct decision grows of course with experience in ecological work.

As a means to the investigation of a definite problem charts are often indispensable. This applies especially to the study of succession or change in vegetation from year to year. The chart then becomes a record or datum with which future records can be compared; and only with their help can succession be accurately and quantitatively studied. We may often *infer* succession by comparing pieces of vegetation and concluding that one represents a later phase into which another will in course of time develop. When a number of obvious transition phases are available, such inferences have a high degree of probability, and most descriptions of successions have in fact been based on this kind of evidence. But at the best these inferences are not so satisfactory as direct observation on the same piece of ground. A succession which is directly traced has a certainty that cannot be impugned, the time required is discovered, the exact details are followed, and the causes of succession are often automatically revealed. The drawback is, of course, that such direct study of succession has to be extended over several or many years; some successions occupy far more than the span of a lifetime. This difficulty may be partly met by choosing different stages of an inferred succession, as represented in different places, and studying each separately by means of a series of charts taken at intervals of time. In this way, if the supposed succession is a real one, the records may be continued until the last chart of one series corresponds with the first of another, and the whole may thus be pieced together.

METHODS OF CHARTING ON DIFFERENT SCALES.[1]

The Gridiron Method.—This has been successfully employed on a very gently undulating salt marsh of which

[1] For descriptions of methods of making vegetation *maps* on scales larger than those of the Ordnance Survey series, see Appendix, p. 199. There is a certain advantage in keeping to the decimal (metric) system of measurement, particularly in the largest scale charts (1 : 10, etc.).

it was desired to chart on a large scale (1 : 60) certain interesting areas. The method is only useful where the boundaries of small well-defined uniform communities can be drawn.

A square (or system of connected squares) is laid down with sides of 25 feet. The corners of isolated squares or systems which will be wanted for future re-charting must be marked by permanent pegs. Iron or seasoned hard wood pegs driven in flush with the soil surface are necessary;

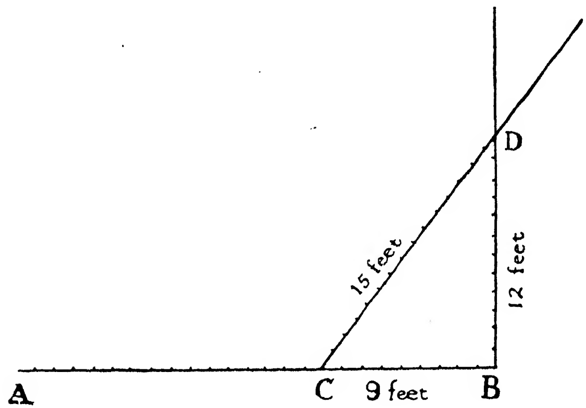


FIG. 2.—Method of determining a right angle on the ground. (See text, p. 101.)

soft wood pegs rot quickly, and may disappear altogether in a year or two. If there is likely to be any difficulty in finding the pegs on a future occasion, the exact location of one at least of the pegs must be fixed by measurement from two permanent objects in the neighbourhood. Much time may be wasted in trying to find the corner pegs of an old square if such precautions are neglected.

which can be plotted on millimetre squared paper. But the practical convenience of using the common English duodecimal system for small scale charts (e.g. 1 : 60 or 1 inch to 5 feet), may outweigh the advantages of decimal uniformity.

When two corner pegs at each end of one side (base) of the "gridiron" have been fixed and a 25-foot tape run between them, a second tape is run from one peg perpendicular to the first. The right angle may be determined by means of a cross-staff or optical square,[1] or if these are not available the right angle can be fixed by the following method (Fig. 2).

If AB is the base of the gridiron and a right angle is to

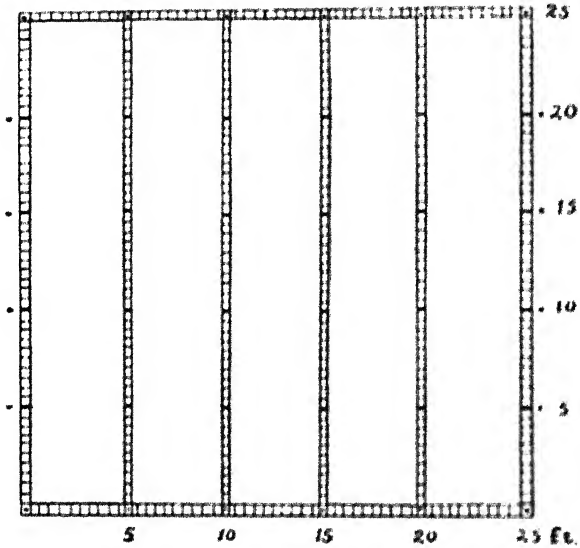


FIG. 3.—Diagram of gridiron tapes as laid out on the ground. The scale of the figure is 1 : 120, or ½ inch to 5 feet. The chart should be made on double this scale (1 : 60, or 1 inch to 5 feet).

be constructed at B, slip the metal loop of a measuring tape on an arrow at B and run out the tape approximately at right angles in the direction BD. Now slip the loop of another tape on an arrow at C, 9 feet from B along BA, and run out in the direction CD. Rotate the tapes BD and CD about B and C respectively until the 15-foot mark on

[1] See Appendix, p. 201.

CD coincides with the 12-foot mark on BD. Fix this point (D) with an arrow. The angle ABD (CBD) is now a right angle.

When the square has been measured out and the corner pegs inserted, the measuring tapes may be replaced by

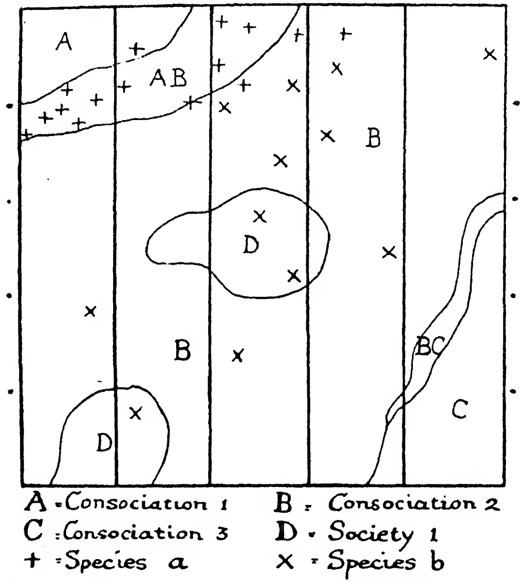


FIG. 4.—Gridiron chart on a scale of 1 : 120 (actual charts should be on twice this scale). The consociations and their transitions, also two examples of a society, are separated by lines, and marked by capital letters (in actual charts these should be the initials of the genera, see p. 104). Vertical and diagonal crosses mark the positions of large isolated individuals of two species. Cf. Fig. 5.

ordinary tapes marked in any convenient conspicuous way at foot intervals and a thin stake stuck in the ground at 5-foot intervals. Four cross tapes also marked at foot and more conspicuously at 5-foot intervals are then run parallel with two of the sides, dividing the square into five strips as with the bars of a gridiron (Fig. 3). The grid tapes should run *across* the maximum number of community boundaries.

The grid is now ready to be charted on squared paper ruled in inches (5 feet on the ground) and tenths of an inch (6 inches on the ground).[1] A square with 5-inch sides and the grid lines at 1-inch intervals are ruled off on the paper, and the charting, which can be done by one person working

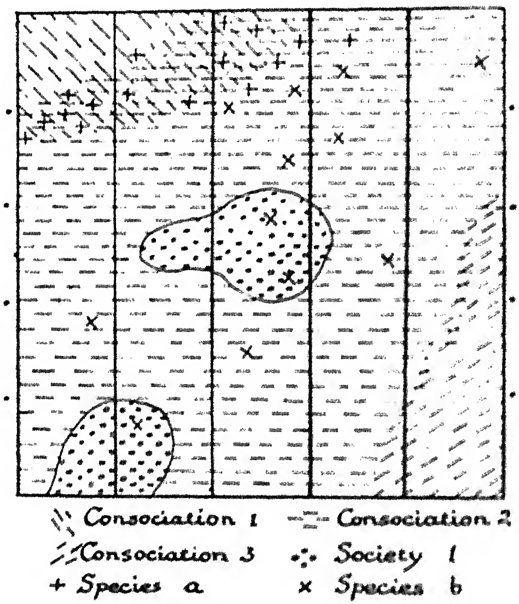


FIG. 5.—Gridiron chart on a scale of 1 : 120 (actual charts should be twice this size). The consociations and their transitions are represented by diagonal and horizontal lines, two examples of a society by dots. Vertical and diagonal crosses mark the positions of large isolated individuals of two species. Cf. Fig. 4.

alone, is proceeded with. The boundaries of the communities are easily and rapidly drawn in pencil. The names of the communities are written in large initial letters (of the dominant genera) on the corresponding areas (Fig. 4).

[1] Books ruled in these dimensions are readily obtained at any good stationer's.

If preferred, the areas may be distinctively shaded. This has the advantage that transitional areas can be easily shown by overlapping two kinds of shading (Fig. 5). The positions of any isolated large plants can be marked by convenient symbols (Figs. 4 and 5). The boundaries, symbols, etc., should afterwards be inked over and the chart kept for reference. The charting should be accurate to about 3 inches on the ground.

If the metric system is preferred, a smaller grid, 5 metres square, may be employed and charted (scale 1 : 50) on a square decimetre of millimetre squared paper mounted at one end of a card 6 inches by 4½ inches (see p. 109) as shown in Fig. 8.

It must again be emphasised that the grid method is only suitable for charting the distribution of sharply bounded communities, and fixing the approximate positions of large isolated individual plants. It may be used for illustrating samples of a vegetation showing these characters, for succession studies, and where the distribution of the small communities can be correlated with some physical factor, such as soil water content, or (in a marsh or fen) depth of water-level below the soil surface.

Charts Showing Individual Plants.

Symbols.—In these charts it is best to use as symbols for marking each individual plant the initial letter of its generic name, and when two or more species of one genus are present to add the initial (small) letter of the specific name in each case. If two or more genera with the same initial are present, a later characteristic letter of the name of all but one must be added. Thus E.c. = *Erica cinerea*, E.t. = *Erica tetralix*, and again S. = *Sanicula europea*, Sc. = *Scilla non-scripta*. The symbols used must always be clearly explained at the bottom or on the back of the chart.

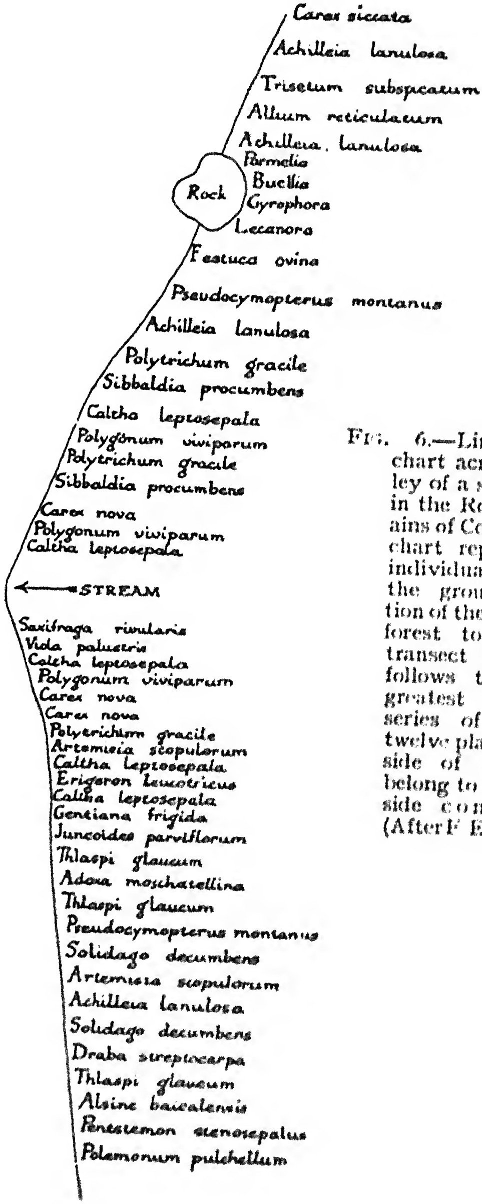


FIG. 6.—Line transect chart across the valley of a small stream in the Rocky Mountains of Colorado. The chart represents the individual plants of the ground vegetation of the pine-spruce forest touching the transect tape, which follows the line of greatest slope. A series of eight to twelve plants on each side of the stream belong to the stream-side community. (After F. E. Clements.)

The Transect.

This is the name given to a line or belt of vegetation selected for charting. The scale is in general larger than that of the gridiron chart, and the individual plants are shown by appropriate symbols. The transect is particularly useful when the vegetation is zoned, i.e. when it forms more or less regular successive zones representing different communities. This arrangement may be in relation to a regular change in physical factors of the habitat (e.g. decreasing water content on the edge of a lake) along the line perpendicular to the extension of the zones. Again, it may indicate a progressive invasion of plants into a community from one side, without perceptible change in the habitat. The transect is made at right angles to the zones, i.e. in the direction in which the habitat factors show the maximum change, or in the direction in which invasion is proceeding.

The advantage of a transect chart is that it shows a definite *range* of vegetation, and by re-charting the transect at suitable intervals of time any progressive change in the vegetation along the line of the transect can be detected and measured.

The Line Transect (Fig. 6).—This is the simplest and quickest form of transect to chart. It is made by running a measuring tape along the desired line, and marking the positions of the individual plants touching the tape on one or both sides, writing their names or the appropriate symbols on one or both sides of a corresponding line drawn on a page of squared paper, or on a square decimetre mounted on card (see above, under gridiron method). Several sections of the same transect can, of course, be plotted side by side on the same page or card.

With regard to the scale of the transect chart this must vary according to the size of the individual plants and the closeness of the vegetation. If it is only desired to record the individual trees and shrubs in a wood, for instance,

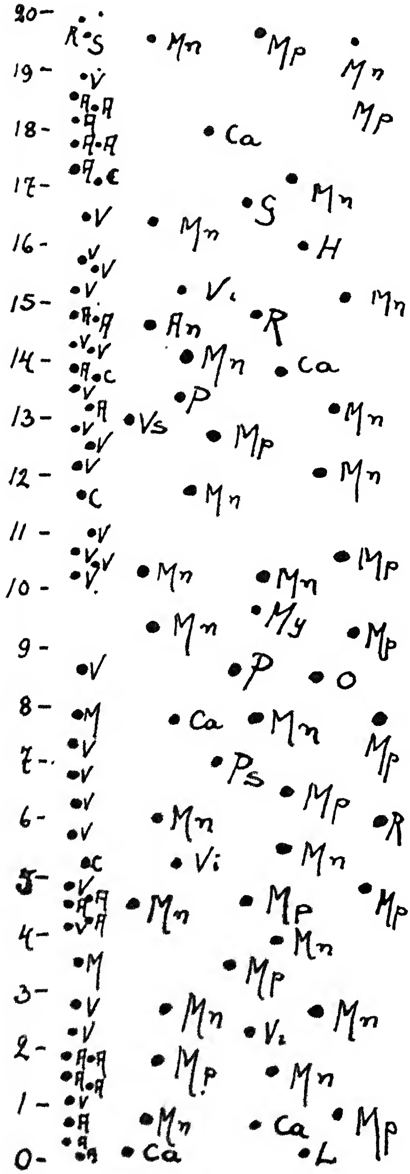


FIG. 7.—Belt transect chart of the under-shrub and herbaceous vegetation of a mossy spruce wood in Norway. The figures represent decimetres. The left-hand column represents a belt about 2 centimetres wide, i.e. practically a line transect, and contains records of the five commonest species only, with a great preponderance of *Vaccinium vitis-idæa* (generally dominant) and *Aira* (*Deschampsia*) *flexuosa* (locally dominant). The rest of the chart represents a belt 5 decimetres wide, and contains records of the less common species only. (From Arrhenius.)

1 : 50 or even 1 : 100 may be a large enough scale. If we are dealing with herbaceous vegetation, 1 : 10 is very often suitable, except where the plants are very small, for instance crowded annuals springing from seed on fallow soil or on certain areas of salt marsh, and here a scale of 1 : 5, or even 1 : 2 or 1 : 1, may be necessary. A scale large enough to prevent the overcrowding of symbols should always be chosen.

The Belt Transect (Figs. 7 and 12) is a strip of vegetation of uniform breadth, for instance a decimetre, 6 inches, a foot, a metre, or even more. It is bounded by two parallel tapes, and the vegetation included between them is charted. For the trees of a wood a metre may be too narrow for the transect—5 metres may be necessary—for a very close uniform herbaceous vegetation of small plants a decimetre may be quite broad enough. The charting scales will be the same as those of the line transects.

The method of charting is the same as for a *quadrat* (see below). The belt transect chart to a certain degree combines the advantages of the line transect chart and the quadrat chart. While it is designed mainly to show the detailed changes of vegetation met with in passing along the line of the transect, it also gives width enough to show the distribution of the individual plants in two dimensions.

The Quadrat.

A quadrat is simply a square patch of vegetation of any desired size enclosed within four tapes or laths for purposes of record. The simplest kind of record is a list of the species enclosed within the quadrat. To this may be added the number of individuals of each species. A large number of such list quadrats taken at random from, but well distributed over, a typical area of an association or consociation are very useful in determining its general percentage composition.

The Quadrat Chart.—For a more complete record of

the community, and especially for the study of succession, it is necessary to chart the quadrat, the position of each individual plant being entered on the chart.

The standard size is taken as one square metre, and for herbaceous vegetation this is plotted on a scale of 1 : 10, i.e. on a square decimetre of millimetre paper such as is sold for drawing graphs. This can be conveniently mounted

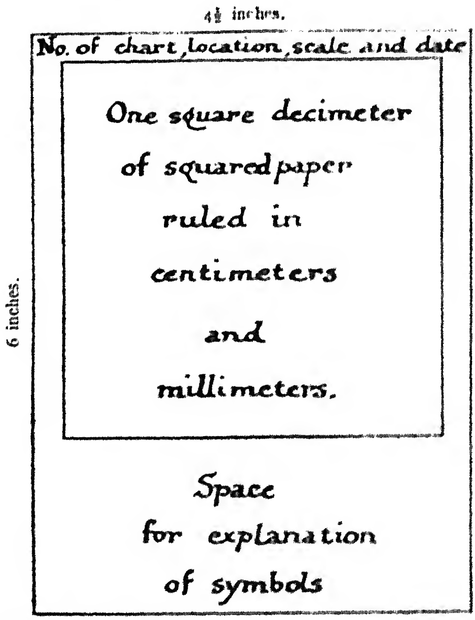


FIG. 8.—Diagram showing method of mounting blank quadrat chart on card. The diagram is one-half (linear) of the original.

at one end of a card cut to 6 by 4½ inches (as shown in Fig. 8), such as are used for mounting the field sections of Ordnance maps (see p. 84). The margin of about a quarter of an inch on three sides of the actual chart is convenient for writing scale numbers, date, etc. Below the chart about 1¾ inches of card are available for the name and location of the quadrat, and the names of the plants with

the symbols used. These can, if necessary, be continued on the back of the card.

The boundaries of the quadrat are made with tapes or laths pegged with meat skewers or surveying "arrows" at the corners. The boundary tapes or laths should be marked in decimetres.

In charting it is well to have a wooden metre scale, and to lay this parallel with and one decimetre from the bottom boundary lath or tape, thus cutting off a strip a decimetre broad. A blank chart or decimetre scale may then be laid a decimetre from the end of this strip so that a square decimetre of vegetation is enclosed. The charting of this square decimetre on the corresponding square centimetre of the chart is then proceeded with, and when finished the decimetre scale is moved a decimetre along the strip and so on, until the strip is completed, when the metre scale is moved another decimetre up, and so on until the whole quadrat is charted. In this way, i.e. by charting a square decimetre at a time, the maximum of ease and accuracy is obtained. In charting each square decimetre the "joins" with the adjacent ones already charted are checked by the symbols already made. By starting at the bottom and working upwards injury to the plants by lying on them before they are charted is avoided. These precautions are very necessary when working with dense vegetation to which the eyes must be brought very close. If the quadrat is to be photographed this should be done before the charting is begun for the same reason.

For very close vegetation, consisting of a great number of individual plants in a small area, the scale of 1 : 10 is not sufficiently large. A scale of 1 : 5 is usually large enough for such communities, though in extreme cases 1 : 2, or even 1 : 1, may be necessary. The chart should be of the same size (one square decimetre), but each square centimetre of the chart will then represent respectively 25, 4, or 1 square centimetre of the vegetation.

On the other hand, quadrats of woody vegetation, for instance scrub or forest, must be much larger than one square metre. Quadrats of five or ten metres square are often large enough, though in a mature forest of large trees even the last-named size may not be sufficient. It is seldom possible to include both trees and shrubs and also herbaceous ground vegetation in the same quadrat chart, because of the very different scales required.

The scale chosen for any quadrat should be such that each symbol occupies about the space corresponding to that covered by the plant represented, so that in a closed community the chart is well filled without being overcrowded, and in a partially open community the proportion of the total space covered by symbols to the total of the gaps is approximately the same as that on the ground.

Tufted or cushion plants, covering a considerable area, should be outlined on the chart. The horizontal spread of the branches of plants casting considerable shade may be indicated by a dotted line. Trailing branches may be indicated by continuous lines starting from the symbol (stock) and ending in an arrowhead. A distinct kind of vegetation, forming for instance a distinct stratum of the community, such as a moss or lichen stratum, may be indicated by a different type of symbol, for instance diagonal or horizontal lines, dots, crosses, etc. Figs. 9 and 10, which show the nature and rate of advance of heath plants during two years on an area which had been bared some years previously, will illustrate the use of these symbols.

It is not of course necessary for all purposes to chart a quadrat by the rather laborious method described, on millimetre squared paper and on a standard scale. Quadrats designed only to show certain features, for instance the number and distribution of the individuals of certain species, may often be charted accurately enough to serve the purpose in a few minutes, and may be of any convenient size and scale, though this last should always be ascertained and

E. Erica cinerea. C. Calluna vulgaris. T Teucrium Scorod

Cl. Cladonia sp. R. Rubus fruticosus G. Galium saxatile

Ve. Veronica officinalis. Rum. Rumex Acetosella U. Ulex euro

Agrostis canina (stoloniferous). Polytrichum pilif

(the mixture of the two latter is represented diagram

FIG. 9.—Chart of permanent metre quadrat on standard scale (1 : 10), sh a stage of succession from bare gravel to heath association (*Calluna*— *cinerea*). Note the large proportion of the surface covered by *Polyt piliferum* and *Agrostis canina*. Seedlings of *Calluna* and *Erica* are num

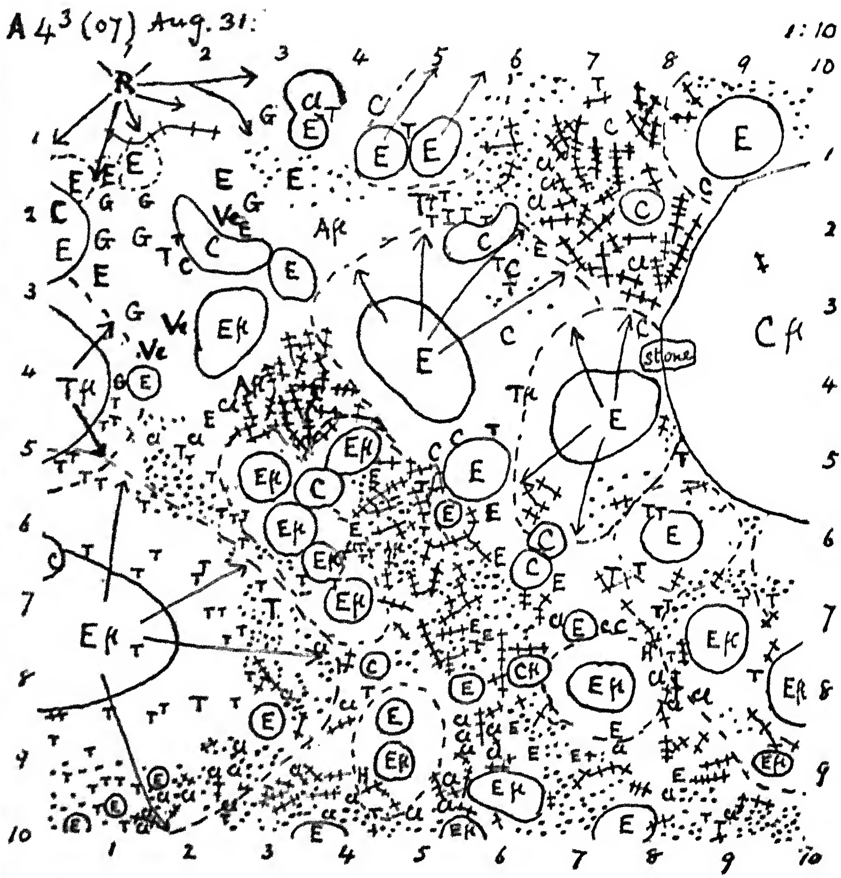


FIG. 10.—Chart of the same quadrat two years later. Note the rapid extension of the two heaths, which now cover the greater part of the quadrat, and the corresponding restriction of *Polytrichum* and *Agrostis*. *Teucrium scorodonia* has also increased greatly, especially in the shelter of the heaths. The few other species are subordinate. Symbols as in Fig. 9. The suffix *fl* means that the individual plant is in flower. The continuous lines indicate the outlines of the tufted plants, the interrupted lines the limits of the shade they cast.

noted. For such purposes a notebook with paper ruled in tenth or quarter inch squares is convenient. It is for the accurate recording of the whole of the vegetation of typical samples of a community which is being studied, and especially for obtaining the data for detailed successional studies, that standard paper and scale, and careful thorough charting are required.

For successional studies the quadrat must be made permanent, and this should be done in the way described on page 100, namely by driving in flush with the ground-level at least two (preferably all four) corner pegs of metal or well-seasoned wood, and then measuring or reading the angles made by lines drawn from the quadrat to at least two objects in the neighbourhood which are at once conspicuous and permanent.

Profile Charts.

The Stratum Transect.—This is a profile of vegetation, drawn to scale, and is primarily intended to show the relative heights of the plant shoots. It is based on the line transect, and is the complement of the belt transect (p. 108). The line transect shows the distribution in one dimension, the belt and stratum transects in two, the profile or stratum transect including the vertical dimension. It is made by running the measuring tape along the line of the desired transect, and measuring with a wooden metre or foot scale, held vertically, the heights of the individual plants touching the tape. In some cases it is convenient, and conduces to rapidity of drawing, to fix one or more horizontal strings or cords, attached to vertical stakes at definite heights (according to the height of the vegetation) above the measuring tape. "Sag" must of course be avoided or allowed for.

The lateral spread of the individual plants at different heights should be indicated on the stratum transect chart.

This is best done by a conventionalised representation of the plants of each species (Figs. 11, 12).

The Bisect.—This name is given to a stratum transect

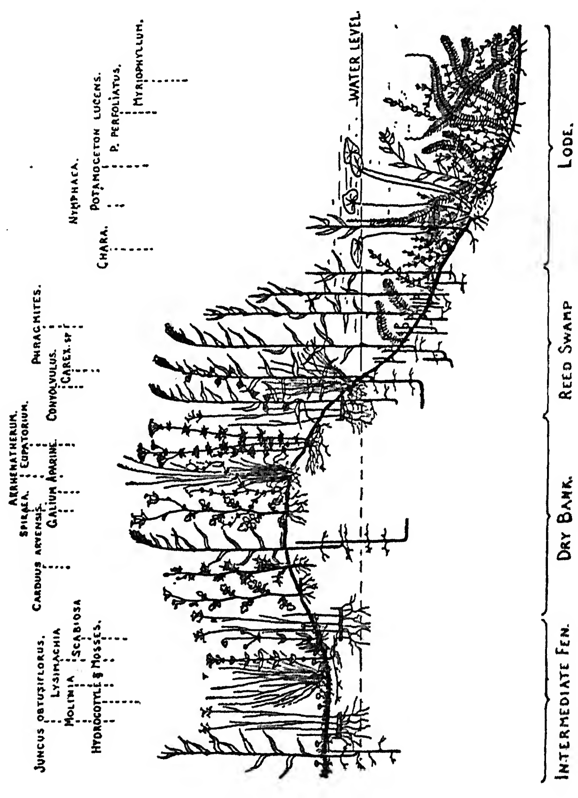


Fig. 11.—Bisect through edge of fen, bank and lode (drainage ditch) at Wicken Fen, Cambridgeshire. Scale, 1 : 60. (From R. H. Yapp.)

chart which includes the root systems as well as the shoots (Figs. 11). In making a bisect chart the shoot systems should first be plotted as described above. A trench should

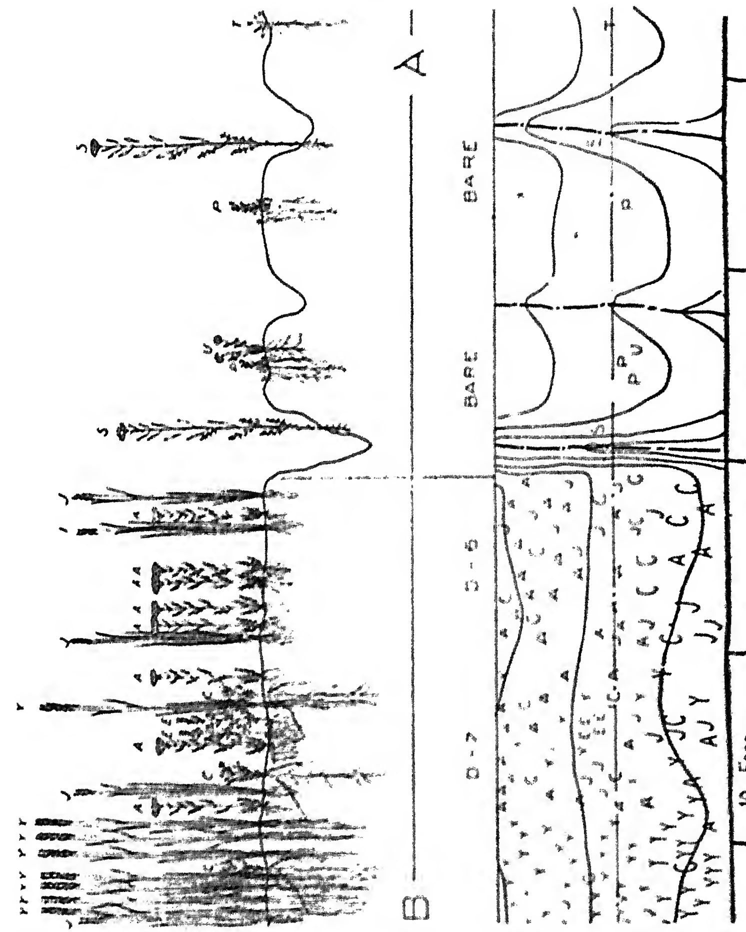


FIG. 12.—Belt transect and bisect charts in grassland used as cattle-range at 10,000 feet altitude on the Wasatch Mountains in Utah. On the left the slender wheat grass (Y) consociation is intact; on the right the vegetation is destroyed, the ground eroded, as a result of heavy overgrazing, and occupied only by a weed community. Contour lines 1 foot apart vertically. (From Sampson.)

A, *Achillea lanulosa* (yarrow).
C, *Chrysothamnus lanceolatus* (yellowbrush).
E, *Artemisia discolor* (sweet sage).
J, *Stipa minor* (small porcupine grass).

then be carefully dug by the side of the transect line, to a depth greater than that of the deepest root system, the root system of each plant carefully isolated, and its vertical depth and lateral spread plotted to scale on squared paper. Great care has to be used to avoid breaking the finer ramifications of the roots.

The work of making a bisect chart is, of course, very lengthy and laborious, especially so where deep root systems are involved. It is often quite impossible to undertake, if only because the digging of the necessary trench would not be allowed by the owner or occupier of the land. Nevertheless, the accurate recording of the distributions and mutual relations of root system is of very great value. We are still exceedingly ignorant of the facts of root structure and distribution in many of our commonest plant communities, and these facts are of the first importance in any understanding of their economy. The results already obtained in America fully demonstrate the interest and importance of this line of work.

In spite of the obstacles and difficulties, then, the importance of this largely unexplored field must be pressed on the attention of students. Its intrinsic interest and the knowledge that he is in two senses "breaking new ground," will amply repay the enthusiast who will face the trouble and labour of the undertaking.

It is not necessary to chart the root system of every plant on a long transect in order to obtain good results. The distribution and relations of the roots of a few individuals of different species on chosen portions of the line will give much information, and similar useful work may be done in connexion with quadrat charts quite apart from a long bisect.

P, *Pentstemon procerum* (blue foxglove).
S, *Sophia incisa* (tansy mustard).
T, *Taraxacum* (dandelion).
Y, *Agropyrum tenerum* (slender wheat grass).

General Remarks on the Use of Vegetation Charts.

Before leaving the subject of the charting of vegetation it will be well to insist once more on the objects of making charts. The general object is, of course, to obtain accurate records of the facts of structure of plant communities, just as the drawing of the external forms and internal structures of a species of plant is necessary to give us knowledge of the facts of specific structure. That plant communities have definite structures, constant within certain limits, is a fact of which anyone can satisfy himself by carefully examining any stable community. And a knowledge of this structure is essential for understanding the economy of the community, just as a knowledge of the structure of the plant is necessary to understand its economy. We are therefore justified in aiming at accumulating accurate records of the one as of the other, and graphic records are the most accurate and instructive.

But just as the aimless drawing of casual sections under the microscope is of little value apart from the practice and experience the exercise gives, so the same thing is true of charting plant communities. In both cases the sample objects to be graphically represented must be chosen with a definite end in view if they are to be of the greatest value.

In the field of plant anatomy, if the general structure of a new kind of plant is not known, we want to have an accurate record of it, though the structure of some species is more interesting than that of others. And in the same way we want accurate records of the structure of all the well-defined plant communities we meet with in nature. This systematic recording by means of the appropriate charts is therefore a legitimate end in itself. It serves as a supplement to the general maps and descriptions which are all that can be undertaken in extensive work, just as microscopic anatomy serves as a supplement to descriptions and drawings of the external forms of plants.

But the communities of natural and semi-natural vegetation that we actually meet with differ from individual plants in that many of them are not stable organisms but transitory phases, which if left alone will develop into stable climaxes. To chart promiscuous samples of these without knowing their status is so much wasted time and labour. We get no sort of information that we can relate to anything else. As a matter of systematic record, then, our aim should be in the first instance to collect sample charts of the structure of the climax communities.

This sort of work, however, does not appeal to everyone, any more than does systematic plant anatomy. It is, in a certain sense, superficial work, because its end is systematic record rather than the opening of an avenue to the formulation of problems. And just as the plant anatomist may prefer to make a detailed study of the structure of a single species, and his interest may be centred in that structure as a working mechanism, so the interest of the student of vegetation may be centred in the intensive study of a single association or consociation with a view to learning how it came into existence and how it maintains itself. He will then not only record its adult structure, its variations, and the conditions under which it exists; he will also try to find out how that structure came to be built up, and its relationship to the communities which precede it in succession under different conditions. During such a study all kinds of problems will turn up, and their solution may be attempted by various methods. Among the methods which will have to be employed, charts will certainly be necessary, and selections from the most suitable of those described in this chapter may be made. For any thorough study of succession, as already noted, detailed quadrat or transect charting is essential, though certain successional problems relating to single species may be solved by less thorough methods.

Finally, a word may be said here about the great

educational value of quadrat charting to the student himself. Quadrat charting forces the attention to the details of vegetation exactly as drawing a section under the microscope forces the attention to the details of tissue structure. No one can become an expert plant anatomist unless he has given the continuous attention to details of plant structure which is involved in learning how to draw and in constantly drawing microscopic sections; and no one can become an expert in the finer structures of vegetation unless he has given them the same kind of attention, which is involved in the effort to represent them graphically. In both cases there is the danger of falling into routine, of making the graphic record the end in itself; in both cases the mind should always be kept open to the problems raised by the detailed facts of structure observed.

CHAPTER IX

INTENSIVE STUDIES (*Continued*). INDIVIDUAL SPECIES AND THE PARTS THEY PLAY IN FORMING COMMUNITIES

It was said in Chapter III that the study of a plant community always and necessarily drives us back to the individual species, and we begin to realise how little we know about them One of the first things of which we realise our ignorance is the life history of the different species in relation to the conditions under which they actually grow in nature.

Maintenance and Dispersal of Species.—Take, for instance, the ground vegetation of a wood. What do we know of the actual means by which the different herbaceous species maintain themselves from year to year, or spread from one place to another? In the case of any given species, does it regularly ripen seed? and if so, does the seed fall and germinate, and do the seedlings establish themselves and grow into plants, which flower in their turn? Is seed spread to new areas, and does it thus increase the distribution of the species? All these questions require specific answers based on exact observation, for the process of reproduction by seed may be interrupted at any point in the series of processes.

The maintenance of perennial species—and nearly all woodland plants are perennials—is effected by the persistence of the original plants from year to year or by the outgrowth of rooting offsets, or by some other means of vegetative reproduction. In addition to this, new plants may be

produced, so far as there is room, by seed falling and germinating among the parent plants. On the other hand, dispersal from one place to another must take place by the actual carrying away of some part of the parent plant, and in the great majority of cases it is the seed which is so carried. Does such dispersal occur, and if so what are the carrying agents?

We are taught that many seeds or fruits have definite aids to dispersal; for instance, plumes or wings, which by offering a greater surface and therefore increased resistance to the air cause the seed or fruit to fall more slowly to the ground, and thus enable it to be carried further by the wind before it alights; hooks or some sticky substance which may attach the fruit or seed to some passing animal, by which it is carried to a distance; or a fleshy envelope which is eaten by a bird or quadruped, the seeds being afterwards voided. There is no doubt that some species *are* sometimes dispersed in all these ways, but it is equally certain that the "dispersal mechanisms" are by no means always effective, that the seeds of plants possessing them are not always carried by the agents (wind or animals) that seem appropriate. We must also take into consideration the vast number of species that have no special "aids" to dispersal.

The questions we have to answer in studying the spread of vegetation are not concerned primarily with general categories of "dispersal mechanisms," but with the actual ways in which particular species are dispersed in particular places; and this is a problem—by no means always an easy one—which can only be solved by direct observation in the field.

It is clear that seeds or fruits which are carried to a distance from the parent plant do not all germinate, or if they do germinate the seedlings may not succeed in establishing themselves. The vast majority of viable seeds that do not find suitable soil in which to germinate are

permanently lost. After a longer or a shorter time the embryo dies. We do not know where they go, because they are too small and inconspicuous to be traced. Sometimes large unmistakable seeds or fruits, such for instance as acorns or beechnuts, may be found lying on the ground in places where they are very unlikely ever to germinate, or, if they do germinate (owing, for instance, to continuous heavy rain), to survive. Young beech seedlings have been found in chalk grassland at some distance from the nearest parent trees, but on a soil so extremely shallow above solid chalk that establishment was impossible. Such cases offer for solution problems of dispersal, even though the result of the dispersal has been ineffective.

The deathrate of seedlings, like that of all young organisms in a state of nature, is enormous. Both beech and oak seedlings, after good beechnut and acorn years, are found in immense numbers on the floor and on the edges of woods. But the vast majority disappear in the course of a few weeks or months. Lately a systematic effort has been made to ascertain the causes of this, and with considerable success (**56** Watt, 1918, **57** 1923, Part I).

The sort of case we often meet with is the colonisation of a new suitable habitat by a species at some distance from the nearest parent plants, while unsuitable habitats at an equal distance remain uncolonised. The most obvious hypothesis to explain this common occurrence is that seeds from the parent plants are spread everywhere, at least to that distance, but that all die except those which reach the suitable habitat. This may very often be true, but it is not necessarily always true. There may be some dispersal factor which takes seed only or mainly to the particular new habitat. For example, a new tree plantation on arable or grassland may receive seed from the woodland plants of neighbouring woods carried by woodland animals or birds, or by carriage on the clothes or boots of woodmen, beaters or sportsmen (**55** Woodruffe-Peacock, 1918). On the

other hand, it is difficult to explain the constant appearance of the common ling (*Calluna*) in suitable new habitats, except by supposing that its seeds are very widely and generally dispersed by the wind or by birds, and that they germinate and establish seedlings only in suitable spots. But direct proof is as yet lacking.

A knowledge of the means of maintenance of a species in a place where it is already established can be obtained by direct observation at different times of the year. Do the already established plants persist from year to year? Do any of them die, and if so, why? Does the species regularly or occasionally produce ripe seed, and do these seeds fall between the parent plants, germinate, and produce new plants which successfully establish themselves? Sometimes all this information can be obtained by simple observation. A permanent quadrat, charted in succeeding years, will give accurate quantitative information as to the appearance of new plants from seed and the disappearance of the original ones.

One method of studying dispersal is by observing the appearance of new species where they did not exist before. In the first place, one has to be quite certain that the species was not present though inconspicuous all the time. After a coppice is cut, for instance, many species which have been dormant or nearly so in the deep shade of the fully grown coppice, represented mainly or entirely by rhizomes or other underground organs, burst into vigorous growth and flowering. Disturbance of an old soil may bring to the surface, so that they germinate, seeds which have been buried, and therefore dormant owing to absence of free oxygen, perhaps for many years. New plantations on old arable land or old grassland, and new specific habitats of all kinds, are particularly favourable for establishing the fact of migration from a distance.

The actual agents of carriage are often very hard to determine. Much can be learned about wind carriage by

observing the transport of winged and plumed seeds and fruits during gales of exceptional force. It is probable that occasional gales are very important in distribution. The distance to which winged and also small light seeds and fruits can be carried by the wind is still a matter of controversy. Close observation of the habits and food plants of animals, both wild animals, especially birds, and also cattle, sheep, and horses will often give a clue that may be successfully followed up. Man himself as a carrier of seeds is by no means to be neglected. But such observation is unlikely to be successful unless a keen taste for it exists in the observer, while long continued practice and unlimited patience are also essential. The study of animal carriage is in fact a special field which only a few born naturalists are well qualified or are likely to enter. Our existing knowledge of the whole subject is extremely fragmentary.

Short distance dispersal can be studied by observing the actual extension of a species from year to year. Favourable cases for investigation have to be looked for carefully: many species in many habitats are practically stationary. When a favourable instance has been discovered, the rate of advance can be measured by permanent quadrats or transects of suitable size on the edge of the area, and the means of dispersal can usually be ascertained in the course of the observations of these. Often the advance is by the growth of rhizomes or runners alone.

Competition and the Establishment of New Conditions.—In a community of perennial plants the number of fresh seedlings that can establish themselves among their parents is limited by the available space. This does not, of course, necessarily mean that the number of plants can increase till the shoots are in lateral contact. The root systems of plants growing spaced out from one another may use all the available water in the soil, so that though there is physically room for more, new individuals cannot establish themselves, though the seeds may germinate. Thus we get

an *open* community in stable equilibrium with its habitat. With a greater water supply, more individuals, of the same and of other species, are able to come in, till eventually we get a *closed* community in which the shoots are in lateral contact. The competition is then for space and light. If tall plants form part of the community, there will be room below them for lower growing plants, and thus we get the beginning of stratification. But these lower growing plants must be able to do with illumination less than full light from the open sky, for some of the light is cut off by the taller plants. When species of several different heights come in, the layering is increased, and in a forest there are commonly four strata: trees, shrubs, herbs and mosses, though in forests (for instance tropical rain forests) very rich in woody species of different habits of growth there may be several more; and where the tree canopy is very dense, so much light is cut off that shrubs and sometimes even shade herbs are unable to grow. As the number and variety of species and the bulk of vegetation increases, more humus accumulates in the soil, and thus gives it a greater water-retaining power, so that the total supply is increased and more plants are able to maintain themselves.

In this way we get increasing differentiation, increasing complexity of the community, somewhat parallel with the differentiation and increase in complexity of an advanced animal or human community, where also there exist different categories of members playing very different parts in the life of the community as a whole, but all dependent on the total food supply available.

Eventually, however, a limit is reached, determined partly by the number of species existing in the neighbourhood, and able to reach the community, and partly by the structure of the community itself. For this excludes species unable to fit into that structure and economy when it is once well established, on account of the limitations of light and water

supply, the constitution of the soil as modified by the existing plants, and other factors. The later stages of development are often marked by an actual decrease in the number of species, since many of those existing in the middle stages of development, where the conditions are intermediate and very varied, are unable to subsist under the ultimate more extreme and more uniform conditions, for instance the deep shade of a wood in close canopy.

The processes which have gone to the making of such a complex community, given the power of arrival of the species which compose it and the general nature of the habitat, are two: competition and the establishment of conditions by some of the species which enable certain other species to exist. Generally speaking, the members of different layers do not compete, because their shoots and very often their roots occupy different strata. It is the business of the student of vegetation to study these processes and to trace out in detail exactly how they lead to the building up of the community (**57** Watt, Part II). It is well to start with a preliminary attempt to understand, in a general way, the structure and economy of the climax, the adult community, just as in studying a species of organism it is well to start from the adult form. But we cannot fully understand the significance of all the features of an adult except in the light of a knowledge of its development. The forces which go to the maintenance of the delicately adjusted equilibrium of a complex organism or a complex community cannot be estimated until we know how they come to be so adjusted, for they are largely masked by the adjustment itself. That is why the biologist insists on the importance of the study of development, and the ecologist on the study of succession—the development of vegetation.

It is impossible to give a detailed account of the methods to be employed in this study. Charting of the various kinds described in the last chapter is essential for an

accurate and detailed knowledge of the structure of the various stages, and the information obtained in this way often leads straight to a closer understanding of the processes involved in succession—competition and the establishment of new conditions. But observation of the facts of succession is constantly making us ask what precisely, in quantitative terms, are the modifications in conditions which lead to the disappearance of one species and the appearance of another, for it must be remembered that every change of conditions affecting the life of plants can be expressed ultimately in terms of chemistry and physics. In other words, we want to measure the change in habitat factors and to determine which are effective in changing the community. We can often guess at these changes, more or less plausibly, but the unravelling and strict proof of the effectiveness of the different factors involved is not an easy or a straightforward task. The habitat factors are considered in succeeding chapters, but for their complete elucidation long continued work, requiring special laboratory training, is necessary, and this is not within the range of the beginner. Some of these problems, indeed, the most advanced contemporary science is as yet unable to attack with success.

Meanwhile an immense amount can be learned, and much of it has not yet been learned, by a thorough study of the facts of succession, aided by quite simple and straightforward observations on habitat, and wherever possible by field experiment. The beginner need not therefore be in the least discouraged because he has no special training in physical and chemical methods, and is unable to conduct difficult laboratory analysis. There is more than enough for him to do without troubling himself about such advanced work.

The possibilities of field experiment to determine crucial points are practically unlimited, and field experiments have not, in the past, been nearly enough used. Thus

where there is a suspicion that water supply is crucial, small patches of ground can be artificially drained or watered (**33** Farrow, 1917, IV; **30** Jeffreys, 1917, III), and though this procedure does not in itself give quantitative results, it does give very valuable qualitative information on this question. The effective value of different intensities of light in excluding or admitting species can sometimes be tested by sowing seeds in variously shaded parts of woods and noting their germination and subsequent growth. Some plants can produce seedlings, but cannot permanently establish themselves under certain degrees of illumination. Others can vigorously develop their vegetative organs, but cannot flower or cannot ripen seed. If the plants flourish and set seed perfectly well, some factor other than light, such for instance as difficulty of dispersal, must be responsible for their absence where there is room and the habitat is otherwise suitable. Many woodland plants can, as we know from common observation, flourish quite well in the open, provided they have a sufficient water supply and the air does not become too dry during their growing season. It is impossible in the field to separate the drying effect from the illuminating effect of direct sunshine.

In all such experiments it must be remembered that the nature of the soil may play an important part. A given water supply which is adequate on one soil is quite inadequate on another, because less of the water is actually available for root absorption (see Chapter XI). The effect of animals can often be determined by preventing their access in various ways (**33** Farrow, 1916, II; **56** Watt, 1919, **57** Part I).

In this chapter we have done no more than touch upon some of the main problems raised in the intensive study of vegetation, but it is hoped that enough has been said to enable the student to realise some of the ways in which the study may best be approached.

PART IV
THE HABITAT

CHAPTER X

THE HABITAT. CLIMATIC AND PHYSIOGRAPHIC FACTORS

In modern ecological work the term *habitat* may be taken to mean "the sum of the effective conditions under which the plant or the community lives." Originally it meant the *place* in which it lives,[1] but while the word is still commonly, and of course quite legitimately, used in this sense, it has now become a scientific term applied to all the conditions affecting the plant incidental to the place in which it lives. Thus we have to distinguish the general habitat of a community from the particular habitat of an individual plant belonging to it, for it is at once obvious that the conditions under which an oak tree lives are different from those of the moss growing upon its bark, though they have some points in common, for instance the general climate of the locality. (Cf. **54** Yapp, 1922).

Every species and every community has a certain *range* of habitat, which may be wide or narrow. Thus some species are distributed over a large portion of the globe under a considerable variety of climates, others are confined to a very restricted set of conditions, which may be realised only within a small area. It by no means follows that such a species *can* only live within the area to which it is actually

[1] From the Latin *habitat*, "it lives in" or "inhabits," e.g. *Primula habitat in silvis*, the primrose lives in woods: hence the habitat of the primrose is woodland.

confined. It may not have completed its natural migrations, and may still be in course of extending its range. All species *tend* constantly to increase their range, and it has been shown that the areas covered by species vary *on the whole* with their *age*, i.e. with the time during which they have been in existence.

But this tendency is by no means always realised. A species may be prevented by various kinds of barriers—oceans, mountain ranges, deserts, etc., or closed plant communities which it cannot enter—from spreading from the place to which it is in fact restricted, though if it is transported across these barriers to a suitable spot it will establish and propagate itself. This is well seen when European plants, especially "weeds," which have great powers of dispersal,[1] are transported to temperate North America or to New Zealand, or plants from the Old World tropics are carried to those of the New World, and *vice versa*. Thus we may distinguish *actual* from *potential* habitats.

The same is true of communities, though in a much more restricted way, for a whole community has not the mobility of the single species.

Theoretically, of course, we should be able to analyse the different factors of the habitat into the ultimate physico-chemical forces acting upon the different organs and cells of the plant, but we are as yet far from being able to do anything of the kind: neither plant physiology nor physical chemistry is sufficiently advanced. Even the most highly trained student of habitat factors has at present to be content with comparatively rough statements about the evaporating power of the air, the range of soil water content, percentages of various mineral salts, hydrogen-ion concentration, and

[1] Due to a variety of causes. They commonly grow quickly and produce a large amount of seed in a short time; frequently their structure makes them easily carried by the wind. Again, they are unwittingly carried by man with crop seed or otherwise. Thus, if a stretch of land in virgin country is ploughed, weeds will appear, though they could not cross the space separating the newly ploughed land from their nearest habitat without the aid of man.

so on, and he is still far from understanding the different interactions of the various factors, or their exact effects upon plants of different structure and different types of metabolism. All this is of course outside the range of the beginner.

Much of the detailed exact study of the habitat factors is considerably more difficult than equally detailed exact study of the structure and distribution of vegetation. It is partly for this reason and partly because the study of the latter is greatly neglected that special emphasis has, in this book, been given to the vegetation itself. At the same time the student must recognise that he cannot completely understand vegetation unless he acquires some knowledge of the habitat. Here we confine ourselves to the simpler and easier methods of approach to habitat problems. The keen student will gradually acquire a knowledge of the problems that he cannot solve by the simpler methods, and if time and opportunity are available will learn the technique necessary to attack them.

For general purposes we may group habitat factors (ecological factors) into *climatic, physiographic, edaphic and biotic,* though the factors in the different classes are not always sharply separated.

Climatic factors include the general features of regional climate and season, light, temperature of the air, rainfall, humidity of the air, winds.

Physiographic factors are those determined by the general nature of the geological strata, by topographical features, such as altitude, slope, exposure, and by geodynamic processes, like erosion, silting, the blowing of sand, and the like.

Edaphic factors are those dependent on the soil as such, its physical and chemical constitution, water content, aeration, etc.

Biotic factors are those due to living organisms, either animals or plants.

It will easily be seen that the factors assigned to different

classes act and may react upon one another. Thus the climatic and physiographic factors influence one another, and both affect the edaphic and biotic, so that some of these last are largely due to the others.

The factors classed as climatic have a dominating influence upon all the others. Rainfall, together with the lithological nature of the strata ("rocks" in the wide geological sense), determines the size and course of the rivers and streams, and thus the conformation of the land, slope and exposure. Again, altitude, slope and exposure determine what may be called "local climate," affecting the temperature, rainfall, air moisture and insolation (radiant energy from the sun) to which a given piece of vegetation is exposed, and therefore to a large extent the particular species of plants that form it. Further, physiography and climate between them, together with the physical and chemical characters of the rocks, determine the nature of the soils that are formed, and thus the edaphic factors of the habitat.

The direct effect of edaphic factors is also very great, since the root systems of land plants normally inhabit the soil. Both the physical texture and the chemical properties of different soils are important in differentiating vegetation, especially when they are extreme and work in the same direction as the climatic factors (see p. 173).

The biotic factors of the habitat are due to the organisms which directly affect vegetation. Animals act upon plants in various ways, very largely by eating them or parts of them, but also by carrying pollen and seed, and by manuring and otherwise altering the soil.

Plants themselves, as we have seen in earlier chapters, profoundly affect one another, and the effects which they bring about are sometimes included in the biotic factors of the habitat. This use of the term is correct enough when we are considering the habitats of single species, but not of course when we are dealing with a plant community as a whole (see p. 130). Invaders from another community may,

however, so change the habitat of the community as eventually to destroy it.

Community habitats change like the vegetation itself. Apart from general changes of climate and of physiography, the soil may be constantly changing by erosion, rain wash, and silting; and in stationary soils by leaching (the washing out of soluble salts) and by the accumulation of humus. This last process, the most important of all, is one direct reaction of the plant community itself upon its habitat.

Thus we see that the habitat is a very complex thing, the result of the interactions of a host of varying factors. But we must always remember that its actual effect upon the plants (apart from the grosser direct effects of animals and of physical agents, like wind, snow, rushing water, etc.) is resolvable into a few physical and chemical processes—the effect of light on photosynthesis and growth, the effect of temperature on the chemical changes in the plant body, the evaporating power of the air on the water in the plant, the effect of the soil solution and its contained ions on the root hairs and through them on the other tissues of the plant.

Climatic Factors.

1. Light.—No completely satisfactory method of determining the varying light intensities in different habitats, and especially the *different* light intensities and qualities effective in plant metabolism, has yet been devised. There are great difficulties in the way of measuring the light as it actually affects green plants. One of these is that light is essential to the life of green plants in more than one way. It provides the energy for photosynthesis, and it affects growth, probably in different ways; it also has a specific effect in the promotion of flowering. The particular rays of the spectrum which are most effective in these diverse functions are different. The ordinary methods of measuring light depend on its effect on chemical reactions, and the rays which are most active in these are not the same as those

most active in photosynthesis. Though the chemically active rays (blue end of the spectrum) are on the whole those which affect growth and flowering, we do not know that their intensity, as measured by any chemical change which is convenient for record outside the plant, is exactly proportional to the intensity of the light effects upon the plant.

Nevertheless, measures of the rapidity of darkening of photographic paper are certainly useful for rough measures of the "light" of a habitat at any given moment. It has been shown that there is considerable constancy in the depth of shade, as measured in this way, that a given species will tolerate.

An ordinary actinometer such as is used by photographers—for instance the Watkins "Bee meter"—is the simplest instrument to employ. The time in seconds that a freshly exposed strip of the sensitive paper takes to darken so as to match the standard tint in the habitat is compared with the time in the open. Since the time taken in darkening is inversely proportional to the light intensity, the light in the shaded habitat may be represented as a fraction of the light in the open by using the number of seconds occupied in the former in darkening to the standard tint as the denominator, and the number occupied in the latter as the numerator. Thus, if the time occupied in the former is one minute and in the latter two seconds, the light in the habitat is $\frac{2}{60} = \frac{1}{30}$. The readings in the first instance should be made in bright sunlight near midday, the actinometer being held horizontally in the open, and perpendicular to the source of greatest illumination in the shaded habitat. In the middle of a close wood this will also be horizontal, since the greatest illumination is vertical. To neutralise inequalities of illumination which may occur under a canopy of varying density the actinometer may be moved slowly backwards and forwards during exposure over a typical patch of vegetation. The average of several readings will tend to reduce accidental errors. Besides the readings in bright sunlight it is well to take some in cloudy and overcast weather.

The minimum light intensity necessary to the existence of certain species or communities of the ground vegetation of woodland may often be determined by this method, at least for any given type of woodland. If great discrepancies are found between the apparent minimum illumination in different places other factors must be looked for, e.g. incomplete migration, competition of other plants, difference of soil moisture, variation of humus, etc.

It must be remembered that many woodland plants produce their leaves and flowers in the "prevernal aspect" (see p. 38), i.e. when a much larger fraction of the total daylight reaches the floor of the wood than is the case when the foliage of the trees and shrubs has developed. Readings should therefore be made during this "light phase," as it has been called, say in mid-April, as well in the "shade phase" at midsummer. The light of the light phase is certainly very important to the prevernal species, and affects them in different ways, the leaves of some dying off in the shade phase, while those of others persist throughout the summer.

One drawback of the photographic actinometer method of light determination is that it gives records only at the moments at which readings are made. No really satisfactory method of integrating the total light received over a period of hours or days has yet been invented.

2. Temperature of the Air.—Single temperature readings are not of much use, save on exceptional occasions, but if an automatic thermograph, recording the temperature curve on a drum, is available and can be safely set up in the habitat without risk of interference, useful results may be obtained.[1] If in the open the thermograph must be protected from the direct rays of the sun. Sun temperatures are not recorded by the instrument.

3. Rainfall.—Indirectly this is a factor of prime significance for plants, but it is seldom a *direct* factor of importance.

[1] These instruments require a new blank chart to be affixed once a week.

The total rainfall, and especially the distribution of rainfall through the year, is one of the leading features of climate, but sufficiently close figures can usually be obtained from the nearest rainfall station.[1] Where there is strong land relief, however (for instance in mountain regions), the local rainfall often varies very considerably within quite short distances, and additional rainfall records in such places are very useful for meteorological as well as ecological purposes. An automatic raingauge is the most useful instrument. This registers the rainfall on a drum and empties itself automatically when the receiver is full, the pen returning to the base line. Like the automatic thermograph, it requires a new chart once a week, and must be exempt from mischievous interference. For meteorological purposes certain precautions as to location of the gauge have to be observed (as to which the Secretary of the British Rainfall Organisation will give information), but some of these do not apply to the measurement of rainfall in a given habitat.

4. Humidity and Evaporating Power of the Air.—This is a very important direct factor, far more so than rainfall, since it directly affects the function of transpiration (loss of water by evaporation from the aerial parts of the plant), one of the leading functions through which the habitat of a plant is determined.

The commonest meteorological instrument for measuring *relative humidity* (the percentage amount of water vapour held by the air at a given temperature, the amount required for saturation at that temperature being taken as 100) is a pair of thermometers, one with a "wet," the other with a "dry" bulb. The "wet" bulb is surrounded with a gauze envelope connected with a little reservoir of water by a stout strand of cotton fibres, which by capillarity keeps

[1] The British Rainfall Organisation (Camden Square, London) has a number of trustworthy observers scattered throughout the country, and will always courteously respond to a request for local information. Through this organisation any working ecologist can get into touch with the local rainfall observers.

the envelope of the bulb wet as evaporation proceeds. The jacket of evaporating water lowers the temperature of the wet bulb proportionally to the rate of evaporation, so that the difference between the temperatures recorded by the two thermometers is a measure of the deficit of water vapour in the air below saturation point at the given temperature. If the two thermometers show the same temperature, the air is saturated. The drier the air the greater the difference of temperature between the two thermometers. Hygrometrical tables show the relative humidities corresponding with given readings of the wet bulb at given dry bulb temperatures.

Wet and dry bulb thermometers thus record the relative humidity of the air at a given spot at a given moment. A more directly useful instrument for the ecologist is the Livingston atmometer (evaporimeter), which measures the amount of water actually lost by evaporation from the wet surface of an inverted porous (unglazed) earthenware cup. This amount is a measure of *the total evaporating power of the air at a given spot over any period*. By its use we can integrate the water content of the air with the temperature and wind and the time factor. Wind has the effect of raising the evaporating power of air (if it is not completely saturated with water vapour) by constantly removing the saturated air round the wet surface and replacing it by drier air.

The total evaporating power of the air is of first importance to plants. If the roots of a plant are freely supplied with water, the difference between the amount lost by the atmometer surface and by the plant surface, reduced to a standard, is a measure of the checks to transpiration possessed by the plant.

In the Livingston atmometer (the simplest form of which is shown in Fig. 13) the open end of the porous cup is attached to a tube connected with a bottle of distilled water.[1] The

[1] Any impurity of the water fills up the pores of the earthenware and lowers the evaporating power of the cup. Water containing lime does this very quickly. To prevent the growth of algæ the cup may be rinsed with weak corrosive sublimate. The cups may also

cup is filled with water, stoppered and inverted, the tube being introduced into the bottle and the stopper of the latter closed, great care being taken to admit no air into the tube or cup. As the water evaporates from the outer surface of the cup, it is supplied by the rise of fresh water from the

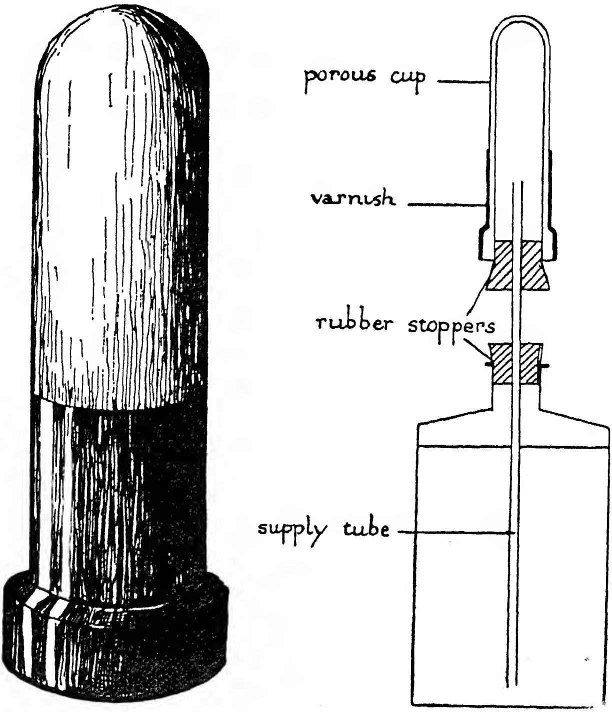


FIG. 13.—Livingston atmometer cup, simple pattern, and section through cup with supply tube and bottle.

bottle, so that the cup is always kept full. The loss of water from the bottle is measured in cubic centimetres when the atmometer is visited, and the bottle is then refilled. The

be cleaned with a stiff toothbrush and distilled water at intervals. The porous surface should never be handled. If these precautions are taken its evaporating power varies very little.

lower part of the cup is varnished so as to reduce the evaporating (unvarnished) surface to a known area.

Owing to the variations of structure of eathenware, different cups have different evaporating powers per unit surface. The different cups can be standardised by comparison with a standard cup whose rate of evaporation under standard conditions is known. In this way each individual cup has a coefficient, or correction factor, which in the cups on sale commonly varies between 0·67 and 0·79, and multiplication of the actual amount of evaporation by this factor corrects the figure to that of the standard cup. Thus a value can be obtained for the evaporating power of the air at any time and place,[1] which is directly comparable with those obtained by Livingston and many other workers in America, where these cups are very widely used. Relative values can be obtained by comparing the records given by atmometers in protected habitats, i.e. where the evaporation is less than in the open, with those of a fully exposed atmometer in the open and expressing the results as fractions, in the same way as the light intensity in a shaded habitat can be expressed as a fraction of that in the open. But unless the cups are standardised, the results are of course subject to the errors depending on the variations of individual cups. In the cups on sale, however, this error is commonly small.

5. Wind.—Violent winds often break off twigs or branches of plants, especially of trees and shrubs, but the most important general effect of wind is to increase transpiration, by constantly bringing unsaturated air into contact with leaves and young shoots of plants. The drier the air and the higher the velocity of the wind the greater is this effect. In its extreme form it can be seen by the "blighting" effect

[1] Livingston atmometer cups cannot be purchased in this country, but they can be obtained from the Laboratory of Plant Physiology, Johns Hopkins University, Baltimore, Md., U.S.A., at $1.10c. each for the simplest type. Standardised cups $1.40 each. $10 and $13 respectively for 10 cups. Simple bottle with stopper and tube, 40 cents; $4 for 10. Various improved forms are obtainable at considerably higher prices. A complete price list is sent on application.

of a strong dry wind on the young shoots of plants, especially of an east or north-east wind (the quarters from which the driest winds usually come in this country) in the spring. Under such conditions the whole of the young leaves and shoots in exposed situations may be killed in a few hours, owing to the loss of water by evaporation being too rapid to be replaced quickly enough from the roots of the plants.

Even under less extreme conditions constant exposure to wind, commonly to the prevailing west and south-west winds, though these are more or less laden with moisture, may be of the first importance in determining the local distribution of species or communities. Certain trees are well known to the forester to be "wind-resistant," either because they are better protected against over-transpiration, or because their twigs and branches are less brittle. Thus the beech is much more wind-resistant than ash or oak, and the latter cannot establish themselves on the exposed south-west sides of woods, while the beech can. In this way the succession of establishment of trees in forest development may be greatly modified locally.

Owing to friction with the soil surface the velocity of the wind increases very rapidly with increased height above the ground, and the effect of this on vegetation is often exceedingly striking. If a strong wind carries sand particles, these add to the drying effect of the wind, itself an *erosive* effect, the sand being driven against the exposed parts of plants, pitting them, and, if the action is long continued, eventually disintegrating them. Wind-driven frozen snow particles have a similar effect, as may be seen on high mountains near the altitudinal limits of tree vegetation. These effects are greatest at a certain small height from the ground, for below this height friction with the ground surface diminishes the velocity of the wind so that it cannot carry the particles, and above a certain height but few particles can rise.

The velocity of wind is measured by special instruments (anemometers) at meteorological stations of the first rank,

and there is a conveniently small portable instrument ma(
in Germany which can be used by ecologists for measurii
the velocity of local winds. But in view of the fact that th
is expensive and not easily obtainable in this country, ai
that the evaporating effect of wind is integrated with oth
factors by the atmometer cup, the student may be contei
with noting the direction and roughly the strength of prevale:
or occasional winds.[1] The main thing is that his eyes shou
be open to the importance of wind, which is sometimes ignor(
or minimised.

Physiographic Factors.

It has already been mentioned that strong topographic
relief (steep hills and deep valleys) has a profound effect (
vegetation, very largely because it produces characteris!
"local climates." This effect is much more strikingly mark
in less equable regions than Great Britain, whose climate
on the whole very uniform.

Thus, to take one striking example from Southern Euro]
the limestone ridge of Sainte Baume, in Provence, which ru
east and west, bears on its north and south faces total
different vegetations in which there is not a single spec
in common. The lower part of the steep northern face, (
which fog often forms and which is entirely protected frc
the midday strength of the Mediterranean sun, bears virg
beech forest, with holly, yew, abundant lichens and a hygi
philous[2] ground vegetation. The south face is occupi
by the highly xerophilous[3] Mediterranean "garigue" vege!
tion of shrubs and herbs, whose leaves are strongly protect
against evaporation. This complete contrast is entirely d

[1] The "Beaufort scale," used by meteorologists to express t
varying strength of wind, has 13 degrees from dead calm (0) to hui
cane (12). With a little practice the different degrees can be estimat
subjectively. Thus a gentle breeze (3) just keeps leaves and sm
twigs in constant motion (6 miles an hour), a gale (8) breaks off tw
of trees and occasionally impedes walking (30 miles an hour).

[2] Greek ὑγρός (hugros), moist, and φίλος, loved.

[3] Greek ξερός (xeros), dry.

to local climates only separated by three or four hundred feet of rock face.

Similar differences, though seldom so extreme, are seen everywhere except in the most arid and in the wettest regional climates. In the northern hemisphere, northern slopes usually bear a vegetation adjusted to damper conditions than southern slopes, and often the same communities as are borne by the southern slopes at a higher altitude. Generally speaking, the greater the altitude the damper the climate, except in the interior of great continental mountain complexes. In Great Britain such differences are not, on the whole, very well marked; but the vegetation, particularly the subordinate vegetation, of a deep sheltered ravine differs considerably from that of a neighbouring exposed slope. The effect of shelter on windy coasts and mountains is very pronounced. It has also been shown that local climate varies considerably within a few feet or even inches on very uneven ground; the shelter of a small rock or hillock sometimes making a difference, for instance to wind effect, that enables a plant or small community to grow which cannot exist outside the sheltered area.

Steepness of slope, especially in comparatively high latitudes, increases the effect of aspect or exposure. Thus in the northern hemisphere a steep southern slope will receive the rays of the midday sun almost or quite perpendicularly, while a steep northern slope may receive only oblique rays in the morning and evening, or none at all except perhaps for a short period at midsummer. A simple home-made clinometer is a useful instrument for measuring the angle of slope in a hilly country, and with compass bearings the maximum possible time of direct illumination can be calculated, if desired, with the aid of the necessary astronomical data.

The nature of the underlying rock is often reckoned as an edaphic factor, and so it may be; but in so far as it determines topography it is physiographic. Different types of crystalline rocks, hard and soft limestones and sandstones, stratified

shales and unstratified clays, alluvium of different kinds, may produce different topographies, and thus, in conjunction with the climate, affect the physiographic factors. A discussion of such matters belongs to physical (dynamic) geology, some knowledge of which (and the more the better!) is necessary to the ecologist in most areas.

In areas of relatively mature land structure, such as we have in the Midlands and the south and east of England, the topography is changing very slowly. The land forms are relatively static, and geodynamic changes are not now altering the conditions of vegetation except locally and on a small scale.

It is otherwise in mountain districts and on the seacoast, where geodynamic agents are active. Here the topography may be constantly shifting, destroying the habitats of some communities and creating new habitats. Rock faces, steep slopes, and river banks that are being eroded present a special class of habitat on which certain species maintain a precarious existence. If the erosion is rapid enough no species may be able to secure a foothold. Streams cut back into plateaux, increasing the drainage and diminishing the water content of the soil. The eroded material, gravel, sand or clay, or a mixture of these, is brought down by the stream and deposited as silt along its lower course, or creates a delta where the stream flows into a lake, thus providing new habitats for vegetation of different types. Frost, again, breaks up the rocks on flat exposed mountain tops, producing the special type of habitat consisting of more or less loose rocks of various sizes, known to the geologist as "mountain-top detritus." Frost and water between them cause the fall of rock fragments from a rock cliff and thus produce screes at its foot—another type of habitat. All these processes change old habitats or create new ones, and present innumerable problems to the ecologist, both successional problems and problems relating to the factors actually at work in determining the vegetation which appears. The geodynamic factors may, as in the case of an evenly eroding rock face, actually main-

tain a constant type of habitat, and thus a constant type of vegetation, though the individual plants are continually disappearing and being replaced by others.

A parallel series of problems, though some of them are in detail very different, is provided by the seacoast. Here we have on the one hand sea cliffs, composed of different kinds of rock, each of which is being eroded, not only by rain but by the sea, fast or slowly, and is inhabited by certain species of plants, forming various communities. These have, as a matter of fact, been very little studied, but they appear to have a good deal in common. On flat coasts, on the other hand, we have salt marshes, sand dunes and shingle beaches, each type of habitat presenting separate successional and strictly ecological problems. Each of the three may show a straightforward development from the first colonisation of the new habitat, or this may be modified by continual silting with salt mud, continual covering with blown sand, or accretion of fresh shingle; or the habitat may be destroyed at any stage by tidal or wind erosion and the succession started afresh. Or again, as on an eroding rock face in the mountains, the geodynamic factors of tidal or wind action may maintain a condition of equilibrium, and thus a constant type of vegetation.

CHAPTER XI

EDAPHIC FACTORS. THE SOIL. PHYSICAL STRUCTURE AND CONSTITUENTS

EDAPHIC factors are those due to the soil in which the plant is rooted, and it is usually easy to draw a line between these and climatic factors, though, as we have already seen, the characters of the soil are largely dependent upon climate. For example, the soils of a desert would be very different from those of a region of high rainfall well distributed through the year, even if they were derived from lithologically identical rocks.

Relation of Climate and Soil: A Hypothetical Case. —Suppose a well-developed bed of limestone of uniform constitution and with a uniform dip is exposed for many miles across country, and that the climate changes steadily as we pass along the strike of the bed. At one end let us say there is an annual rainfall of 5 inches, at the other of 80 inches—and this is not at all an impossible supposition, for extreme changes of climate within 100 miles, or even less, are well known, though they are not common (apart from high mountains) in Western Europe. In a tropical climate the low rainfall end would be very arid desert, with an exceedingly sparse vegetation of plants highly protected against water loss. The high rainfall end would bear tropical rain forest, the most complex and highly developed vegetation in the world. The soil of the two ends would be totally different, though derived from identical rock. In the desert the rock would be largely bare, and what soil there was would consist of rock particles disintegrated by heat and wind. In the region of high rainfall there would be disintegration of

the rock to some depth, and the comparatively deep soil would be covered by and partly mixed with a layer of humus, and would constantly retain a considerable amount of moisture.

If the outcrop of limestone were preceded and followed by other uniform beds of very different lithological nature, for instance by sandstone and alluvium respectively, also extending into the two extreme climatic regions, it is probable that at neither end of the climatic scale—neither in the desert nor in the rain forest—would the different beds show any very marked difference of vegetation. The extreme climatic factors would dominate the situation in each case. In the desert the species which could just establish themselves in the extremely arid conditions would mostly be able to exist, whatever the chemical nature of the soil, and only some marked physical difference of habitat, such as that presented by rock clefts or sand dunes, would cause a differentiation of the vegetation. In the rain forest the very favourable conditions of plant life would enable a great variety of species to exist, and the particular selection which survived would be determined in the first place by the climate and secondly by the structure of the forest. The climate and all the various soils produced by the different rocks would allow a large margin over the barely necessary conditions of existence.

But in the intermediate region, especially if the rainfall were unevenly distributed during the year, as it nearly always is, so that there were wet and dry seasons, the difference of the underlying rocks and of their reactions to the climate and to the vegetation would probably cause a marked differentiation of the vegetation. With a 20 to 40 inch rainfall in temperate regions, and an even higher rainfall in the tropics, the limestone soils would tend to be dry and shallow, and the chemical effect of the lime on the soil would also affect the vegetation in more than one way. Here then the edaphic factors would be master factors, because they would differentiate the plant communities inhabiting the soils overlying the different types of rock.

The Soil.

The study of the soil as such has become in recent times a separate branch of science. Many books and innumerable papers have been written about it, and in America there is a journal (*Soil Science*) entirely devoted to the soil. It is only within the last quarter of a century that the immense complexity of the processes that take place in the soil and their profound effect on plants have been at all fully realised. The soil of any spot is a true microcosm, a little world, with a physical and chemical structure, an atmosphere, a microscopic flora and fauna of its own; and in this "soil world" one half of the bodies—the roots—of the higher plants spend their lives and do their work, influenced by and influencing the peculiar conditions which are found there, and in turn influencing the aerial parts of the plants to which they belong.

It is impossible here to do more than touch upon some of the features of the soil, and of different kinds of soil, which the field ecologist will first encounter.[1] There is considerable difficulty in doing even this satisfactorily, because we are still largely ignorant of the *exact* ways in which different soils affect plants, and investigation of these questions leads straight to some of the most difficult problems of plant physiology and physical chemistry.[2]

[1] Sir John Russell's *Soil Conditions and Plant Growth* (Longmans, New Edition, 1921, 16s.) is the best English book on the soil, though parts of it are rather too advanced for the beginner. The same author's *Lessons on Soil* (Camb. Univ. Press), suitable for use in the middle forms of schools, is a most admirable first introduction to the subject.

[2] It is important to remember also that most of the work has been done on agricultural soils which are regularly ploughed and profoundly modified by this and other agricultural operations, as well as by manuring and the growth of the crops themselves. In ploughland the *soil* itself, 6 to 9 inches deep, which is regularly turned by the plough, differs sharply from the underlying *subsoil*. Untouched natural soils are very different in many ways, and we do not yet know nearly so much about them, though we are now rapidly learning. One of the most important points in which a natural soil differs from a cultivated one is that in the former there is rarely a *sharp* distinction between soil and subsoil. The ground develops a graded *stratification*,

Physical Structure of the Soil.—Most soils consist of a framework, so to speak, of inorganic particles, derived by disintegration of the underlying rock. According to the constitution of this rock, therefore, the inorganic framework will vary both physically and chemically. Thus a soil derived from a limestone rock will consist largely of particles of calcium carbonate, unless and until "leaching," i.e. the action of rainwater containing carbon dioxide in solution, has dissolved the calcium carbonate from the surface layers and carried it down to deeper levels, leaving behind the insoluble or less soluble particles derived from the rock as well as the organic constituents (humus) of the soil derived from the remains of the plants and animals that live on or in it. This process takes place continually in regions of high rainfall, and especially quickly in very permeable soils. Only where the surface soil is constantly supplied with fresh quantities of carbonate, as for instance on steep slopes where erosion is active or where "hard" spring water irrigates the soil, is a high lime content maintained. Thus the surface layers may be destitute of or very poor in lime, while the deeper layers are very rich, as is the case with many chalk and other limestone soils, and this contrast partly determines the mixtures of vegetation often observed, as for instance on chalk downs, where heath plants, rooted in non-calcareous soil, may be mixed with calcicolous plants rooted in soil which is highly calcareous.

A soil derived from a sandstone or a sand contains a preponderance of comparatively coarse particles mainly composed of silica, whereas clays give rise to fine grained soils of which the very minute particles are composed of aluminium silicates. Many different rocks, however, such as impure sandstones, shales, and various igneous and metamorphic rocks, give rise to soils showing mixtures, in different proportions, of

the top inch or so, for instance, often being very different in character from the layers beneath. In cultivated soil all the surface layers turned by the plough are continually being mixed, so that the whole is kept fairly uniform, down to the level of the untouched subsoil below.

particles of very various sizes. These soils are often generically known as loams—a rather vague term which is applied by gardeners in a narrower sense to a medium soil containing much fibrous humus.

Humus.—The vast majority of soils, all in fact which bear vegetation, contain an appreciable percentage of dead organic matter, which is collectively known as humus. New soils, such as freshly blown sand, or recently deposited silt, and desert soils, which support but little vegetation, contain the least; at the other extreme are the soils which consist wholly, or almost wholly, of altered plant remains, such as peat.

Humus consists mainly of dead plant remains in process of decay, but sometimes decaying animal remains or fæces make up an appreciable fraction. The plant remains consist partly of dead roots and rhizomes decaying in situ, and partly of dead aerial parts, leaves and stems which have fallen and become incorporated in the soil. In many soils earthworms are important agents in incorporating dead leaves with the soil. They drag the leaves down into their burrows, and constantly pass large quantities of humus through their bodies, disintegrating and partially digesting the organic matter. They are aided in this work by other small soil animals, and eventually the disintegrated and decomposed substance is finally broken up by bacteria into carbon dioxide, water and comparatively simple inorganic salts, nitrates, sulphates, and phosphates, mainly of calcium, magnesium and potassium.

These processes take place with the greatest rapidity only in soils with a moderate water content in the presence of plenty of free oxygen, that is in moist, well aerated soils, and such soils are sometimes known as "fresh."[1] When a fair propor-

[1] This is because these conditions (moisture and oxygen) are most favourable to the life of the organisms which carry out the processes of disintegration and decomposition. A comparatively high temperature, also, because it is favourable to the soil organisms, quickens humus formation and disintegration. In cold soils the process is relatively slow.

tion of lime is present, such a soil or its humus is sometimes called "mild," and is the most favourable kind of soil for the rapid growth of plants.

The term humus is sometimes applied to the whole complex of organic matter thus undergoing disintegration and decomposition. The fallen parts of plants (for instance the covering of dead leaves on the floor of a forest), before they have undergone any perceptible change, are, however, conveniently distinguished as *litter* from the humus proper. When the processes of humus formation and destruction are slow (as on cold, dry or acid soils) the slightly changed organic débris, which often forms a thick layer on the surface of the soil and affects the vegetation very markedly, is called *raw humus*. The soils of certain forests and heaths in cool climates, for example most of Northern Europe, are characterised by a layer of raw humus which disintegrates very slowly.

In soils saturated with water the access of oxygen is impeded, earthworms and other animals, which disintegrate the humus, as well as the soil bacteria which require free oxygen, are excluded, and the humus takes the special form of *peat*, in which the structures of the dead plants and parts of plants forming the peat are often preserved. Since no far-reaching disintegration or decomposition takes place, the peat layer continually grows in thickness, and forms the characteristic organic soil of *mosses* and *fens* (see pp. 59–63). There are many different kinds of peat, according to the plants which form it and to the exact conditions of the formation. Broadly, "moss peat" or "bog peat" differ from fen peat in being much poorer in mineral salts and acid in reaction. On moors (in the English sense, see p. 61) and heaths the raw humus forms a thicker or thinner layer of "dry peat." A damp, cool climate tends to increased peat formation and to increased water content, and thus we get all transitions from the thin dry peat of heaths through various types of moor to the very thick peat of the true "moss." In such climates peat may be formed even over a limestone rock, for instance on the

Pennine Hills and in Ireland, except where lime-containing water is constantly supplied to the surface soil. These conditions are very characteristic of most of the hill and mountain country of the west and north of the British Isles. The structural features and chemical composition of heath and moor plants also retard their complete disintegration, and contribute to the maintenance of raw humus or peat, forming a soil suitable for colonisation only by a limited selection of species of the same type. (Cf. pp. 60, 160.)

In strong contrast to the peats and to all the soils which tend to maintain a layer of raw humus, the well aerated soils adequately supplied with mineral salts show, if they are warm enough, a *quick turnover* of humus. Humus is formed in quantity and rapidly because of the favourable conditions for the growth of plants, and it disintegrates and decomposes rapidly, and thus sets free the mineral salts locked up in the plant tissues. The humus itself holds water well, keeping the surface soil moist, and acting as a " mulch " to the underlying layers. These conditions are very favourable to plant growth, and a rich vegetation develops, so that the materials of humus, though rapidly disintegrated, are as rapidly supplied by the plants, as they cast their leaves or die down.

Water Content of the Soil.—The amount of water contained in a given soil at any moment depends on several factors. Soils just above the level of permanent standing or flowing water (" ground water ") are saturated, and the amount of water actually held depends on the constitution of the particular soil. The amount of water at any given time in a soil above the saturation level depends in the first place on the recent weather. After heavy rain, of course, it increases very much, and the surface layer become saturated. The excess of water above the saturation point runs off or percolates through to lower layers. Evaporation of the water begins, but a constantly damp atmosphere retards it. During a long spell of hot weather or of drying winds evaporation decreases the water in the surface layers so much that it

may become "air dry," i.e. the soil water is in equilibrium with the tension of water vapour in the air, so that evaporation stops.[1] A cover of vegetation greatly decreases direct evaporation from the soil, but the soil may lose water more rapidly, and thus become drier by absorption through the roots of the plants and evaporation (transpiration) through their subaerial parts, than directly by evaporation from the soil surface.

But given the same atmospheric conditions (an equal supply of rain water and an equal evaporating power of the air), different soils will retain very different amounts of water according to their constitution. In the first place the humus is a very important water-retaining constituent, and soils rich in humus retain a considerable amount of water (which they absorb and hold like a sponge) for a long time, even in relatively dry air. The extreme case is peat.

Secondly, the amount of water retained depends on the size of the inorganic soil particles. Water *percolates* very readily through gravels and sands, which are mainly composed of coarse particles, and it also freely *evaporates* from such soils because of the large air spaces between the particles. The smaller the particles (and consequently the air spaces), the slower the percolation and evaporation, and consequently the longer the soil takes to dry. Small particles also hold the water in the soil more strongly because of another force, the tension brought into play by the immense aggregate surfaces of all the microscopic particles. A clay soil holds water very strongly indeed, so that the plant roots themselves cannot get out of it nearly all the water present. The result is that much less water is required to saturate sandy soils than clay and humus soils, and also sandy soils retain much less under the same evaporating power of the air. Similarly, plants can use nearly all the water in sand, but not nearly all the water held by clay.

[1] Theoretically, of course, a saturated soil is "air dry," if in contact with saturated air, but in practice we speak of "air dry soil" only if it is in equilibrium with air of "ordinary" relative humidity.

Determination of Water and Humus Content.—In collecting soil samples for determination of water content, it is important to collect from the actual layer in which the absorbing roots of the plants are present. Each sample should be carried in a tin with a tightly fitting lid, carefully marked for identification. The amount of water in a given sample of soil may be determined in two fractions. The soil is first air dried (in comparatively dry air). Ten grammes of the fresh soil are weighed out, spread on paper and left in the sun or (in winter) near the fire and then weighed again. When the weight no longer decreases the soil is air dry, and the water lost can be expressed in decigrams, i.e. as a percentage of the original 10 grammes. The air-dry soil can then be heated in an oven kept at 100° C. and the further loss in weight recorded. This can be expressed as a percentage of the air-dry soil or of the original fresh soil.

The humus (organic) content of the soil is represented by the loss in weight when the soil (previously dried at 100° C.) is heated to redness in a crucible or on a sheet of metal, by means of a flame below.[1]

Size of Soil Particles.—We have already seen that the inorganic particles of a sandy soil are very much coarser than those of a clay soil, and that the "loams" have particles of intermediate size, or a mixture of coarse and fine particles. Natural soils always, in fact, show a mixture of particles of different sizes. A natural sand is so-called because it has a majority of coarse, a clay soil because it has a large proportion of very fine, particles. In order to find out the exact proportions by weight of particles between different limits of

[1] The residue of the humus (ash) does not, except in soils consisting mainly or entirely of humus, appreciably affect the result. Heating to redness breaks up calcium carbonate, and leads to the oxidation of certain chemical substances besides humus; but the weight of these is rarely great enough to alter the figure obtained for humus to any considerable extent. In calcareous soils the carbonate content must be determined separately (see Appendix, p. 212), and the equivalent carbon dioxide subtracted from the loss on burning in order to obtain an approximately correct result for the humus.

size of the larger particles, a natural soil is washed through a series of sieves each with a mesh of definite diameter, and the successive fractions weighed. The smaller particles are determined by the time they take to sink when suspended in water. For the purpose of this process, which is called *mechanical analysis*, names are given to the fractions composed of particles of each range of size. The following are the terms employed in England :—

Above 3 mm.	Stones.
3 to 1 mm.	Fine gravel.
1 to 0·2 mm.	Coarse sand.
0·2 to ·04 mm.	Fine sand.
·04 to ·01 mm.	Silt.
·01 to ·002 mm.	Fine silt.
Below ·002 mm.	Clay.

A rough qualitative analysis of a sample of soil can be made by shaking up 10 grammes of soil in a jar of distilled water or rain water.[1] The sand fractions sink in a few minutes. The silt sinks gradually in the course of a day or so, while the finest clay remains suspended indefinitely. After the sand has sunk the turbid liquid should be carefully decanted off and distributed in several jars, which are then filled up with water and left to stand. The rate of settling and the final turbidity of the water will then give a very fair rough idea of whether the silt and clay fractions of the soil are large or small.[2]

Characteristics of Different Soil Types.—Since most soils contain particles of very various size in different proportions, and also varying amounts of humus, it will be obvious from what has been said above that their relations to water will vary greatly. Thus a sandy soil with mostly coarse particles and little humus dries quickly, and the surface

[1] Water containing lime must not be used because it tends to "flocculate" the clay fraction (see below).

[2] Directions for carrying out a detailed mechanical analysis are given in an appendix to Russell's *Soil Conditions and Plant Growth.*

layers are apt to become too dry for many plants during a period of drought. On the other hand, if the soil is well aerated, if there is an adequate supply of humus and rainfall is frequent, or if (as in many sandy alluvia) the ground water is moving and the level is high, it may be very fertile indeed.

Loams, as already mentioned, are on the whole the best soils, especially if they consist of good mixtures of particles of very various sizes. A considerable "fine sand" fraction, which is very common in loams, ensures adequate aeration, while a moderate clay fraction helps to retain the water; 8 to 16 per cent. is said in this country to be a satisfactory clay fraction in agricultural soils which receive between 20 and 30 inches of rain in the year. Fine silt also has a considerable water-holding power, and if present in excess, especially in company with true clay, it gives a heavy soil. The coarser silts often form a large proportion of good loams. They furnish a useful fraction, tending to keep the moisture even, retarding without preventing the movement of water. The silt particles facilitate the capillary movement of water *upwards* through the soil from the ground water below, whereas the air spaces in the sand are too large, and pure clay prevents the movement of water altogether.[1]

Soils whose clay and fine silt fractions together exceed 30 (and especially where they exceed 40) per cent. are distinctly "clay soils," heavy and expensive to work, and in agricultural practice are usually laid down to permanent grass. The characteristics of clay soils are that they hold water very tenaciously and retard or prevent its movement. They are liable to become water-logged in winter, preventing the ingress of air. In drought they eventually "dry," (though still actually retaining a considerable percentage of water), bake hard, shrink, and crack. They are also cold, "late" soils, because their high water content retards the warming of the soil in the spring. All these qualities make clay soil relatively unfavourable for vegetation. But they are much

[1] Russell, *op. cit.*

mitigated by the presence of abundant humus, which "lightens" the clay, opening it out and allowing the passage of air and water. Above all, the presence of calcium carbonate "improves" a clay soil by "flocculating" the clay particles, and thus again rendering the soil more permeable. The poor aeration of clay soils is well shown by the fact that the grasses of clay pastures are all surface-rooting species, and in a clayey wood the roots of the shrubs are often crowded together close to the surface, while in a sandy wood they are more spaced out vertically and reach a greater depth.

CHAPTER XII

CHEMICAL CONSTITUTION OF THE SOIL

THE first point to be grasped is the fact that the vast majority of natural soils contain plenty of plant food, i.e. more than enough of the soluble mineral salts containing the essential elements N, S, and P, with Ca, K, Mg, and Fe, which plants require for their nutrition, but which they use in very small quantities only. An exception may be found in certain very "sterile" sands, consisting almost wholly of grains of silica; but most unproductive sands are unfavourable to vegetation, not because they are deficient in food, but because they cannot retain a constant water supply. Agricultural and garden soils which are constantly "cropped" require fresh food in the shape of manure, because the nutrient salts are constantly removed in the crops.

The main inorganic framework of most soils consists of insoluble particles of silica and aluminium silicate, which are of no use to plants as food; but mixed with them are particles of various minerals containing the salts more or less soluble in water, whose elements are indispensable to plants. Most of these are ultimately derived from some of the felspars and certain other minerals of igneous rocks. In the stratified rocks they are present in the sediments formed by the deposit of materials derived by erosion and water transport from the igneous rocks. Some of these elements, and especially nitrogen, may be locally deficient in "primary" habitats as yet uncolonised by vegetation, such as bare rock faces, especially of igneous rocks, blown sand, etc.; and this deficiency may contribute, along with the deficiency of water,

to render such habitats difficult and slow of colonisation by the higher plants.[1]

But in soils already fully colonised by vegetation the case is very different. Here the all-important *humus* has been formed, at first by the growth and decay of lower plants (algæ, lichens, mosses), and later by the decay of the dead parts of the higher plants themselves, disintegrated and decomposed by soil animals and bacteria in the manner already described. Actively disintegrating humus, where present, is *the* great source of the chemical food of plants. The mineral salts locked up in the bodies of the decaying plants are set free and rendered available for re-absorption by the roots of the living ones. The organic nitrogenous constituents derived from the protoplasm of their bodies are broken down, and the products successively altered by different kinds of soil bacteria, till *nitrates*, the form in which nitrogen is almost exclusively absorbed by the higher plants, are produced.

This last process, the production of nitrates—*nitrification* as it is called—carried out by special soil bacteria, is of the first importance in humus soils. Thus, if certain kinds of forest are clear felled, the exposure of the soil results in an enormous increase in nitrifying bacteria. This is immediately followed by a great increase in nitrates derived from the nitrogenous constituents of the humus, and then by exceptionally vigorous growth of herbaceous plants, which often cover the ground with a dense mass of vegetation in the course of two or three years. This is partly due to the sudden increase of light, but also to the great increase of available nitrates.

Acid Soils: Importance of Calcium Carbonate. Next to humus and water lime is the most important constituent of the soil from the point of view of its specific effect on the plant communities which can colonise the habitat. Some soils, for instance those derived from the "acidic" igneous

[1] Some of the unicellular plants (e.g. certain bacteria) are able to fix free atmospheric nitrogen and render it available to the higher plants.

and metamorphic rocks poor in minerals containing calcium, certain sandstones, sands and clays among the sedimentary rocks, as well as moss and moor peats, are devoid of, or contain only a trace (a small fraction of 1 per cent.) of calcium carbonate. Such soils, which are known as acid or "sour" soils, require liming if they are to be productive under agriculture, and naturally bear a special natural vegetation, excluding altogether many species of plants, while the limited number that do flourish upon them are often, though by no means always, confined to them. The species that flourish on these soils and avoid those richer in calcium carbonate are commonly known as *calcifuge* species.

In other respects they may make very different demands on their environment, for instance certain species of bog moss (*Sphagnum*) are most intolerant of calcium salts, and they also require abundant water. At the other extreme are species like the sheep's sorrel (*Rumex acetosella*), which flourishes on dry open soils, and is said to be an infallible indicator of poverty in calcium carbonate. Some of the commonest species which are observed to be "calcifuge" in the vast majority of cases (such as *Calluna*, *Erica cinerea*, *Empetrum*, *Deschampsia flexuosa*, *Vaccinium*, and many others), may, however, under certain conditions, tolerate considerable quantities of calcium carbonate in the soil.

We are still largely ignorant of the real deciding factors governing the relations of plants to the chemical constituents of the soil, and here lie some of the most difficult problems of plant physiology and physical chemistry. Evidence is, however, accumulating that the relation depends partly on the "active" acidity of the soil as determined by the concentration of free hydrogen ions, and partly on the relative proportions of the ions of the "basic" elements (Ca and Mg, Na and K) which are present. These basic ions have specific relations to one another and to the roots of plants, also to soil organisms with whose activity the root function of plants is in some case closely involved; and different plant

species vary in their powers of "dealing with" them, according to their own chemical constitution and structure.

It is not surprising, then, that the problems involved are difficult. The term "calcifuge" is at best a rough approximate term to describe a general phenomenon we observe in nature, depending on the fact that it is calcium carbonate, which in nature is the basic salt varying most widely in amount, the other bases being generally present in small quantities only. The term may cover and mask many differences in the detailed relations of plants to the soil. So far from having done with a plant ecologically when we have labelled it a calcifuge, we have to use the observed fact that it usually or always avoids soils containing more than a trace of calcium carbonate as the starting-point for investigation. This kind of investigation requires, of course, a special training.

Mild Soils.—Soils which contain enough calcium carbonate (1 per cent. is often sufficient) to counteract the peculiar properties of "acid" soils,[1] will support a much greater variety of species which no longer belong to a special ecological class. In clay soils calcium carbonate also flocculates the fine clay particles, altering the characteristic behaviour of clay with water. Again, calcium carbonate promotes the action of different soil bacteria which help to bring the nitrogen of the humus and the free nitrogen of the air into forms available for the higher plants.

Calcareous Soils.—Soils with high percentages of calcium carbonate have special characters of their own, not by any means fully understood, but tending to obliterate the distinctions between sands, loams and clays. Correspondingly they bear a vegetation which largely, though by no means exclusively, consists of species characteristic of such soils—the so-called *calcicole* (lime inhabiting) species. We saw that

[1] Either by neutralising definite soil acids which may be present or by altering the ratios of the different bases present, or by saturating the affinity for bases of soil colloids such as peat or clay. There is still difference of opinion as to exactly what occurs in different "sour" soils to which calcium carbonate is added.

some of the calcifuge species were not always strictly limited to soils poor in calcium carbonate, but the calcicoles are a great deal less strictly limited to calcareous soils. It has, indeed, been said that few if any species are entirely confined to calcareous soils in all parts of their range. Nevertheless, in any given region the limestone vegetation is always well marked and characteristic, with a number of species immensely more abundant on, if not strictly confined to, the limestone.

This is the result partly of the chemical and partly of the physical characters of calcareous soil. Limestone soils are frequently shallow and relatively dry, partly owing to the permeability of the underlying rock, partly to the fact that the rock dissolves rather than disintegrates, partly to the rapid disintegration of humus owing to the activity of various soil organisms, including soil bacteria, partly to the absence of colloidal clay owing to the flocculating action of the lime. Many, though not all, of the species characteristic of limestones are also found on other dry soils. These species are in fact relatively "constant" in the limestone communities without being "exclusive" to them (see p. 31). Other species, however, at least within a limited region, are not found on other dry soils but are very nearly exclusively confined to calcareous soils. These latter may, perhaps, be regarded as the "true calcicoles," which are really intolerant of soil acidity. They also *may* grow in other places, provided that the soil is not acid and other conditions are suitable; sometimes, for instance, they are excluded from favourable soils by the competition of other species. There is in fact no evidence that any species *requires* calcium carbonate or calcium, *as such*, apart from the relatively very small amounts required by all plants, and obtainable by calcifuge species even from soils containing but a trace.

The great intolerance of calcium carbonate shown by calcifuge species may also be due to more than one cause. Soil acidity seems to be actually favourable to some species. In others the presence of lime hinders the absorption of potash,

between which and lime there is a marked relation. Many species, not necessarily calcifuge species, show "lime chlorosis" on highly calcareous soils, the leaves becoming pale yellow owing to inadequate development of the chlorophyll. This may be due to the calcium inhibiting the absorption of magnesium, an element which enters into the composition of chlorophyll.

Effect of Competition between Species.—When we consider the great differences between the demands made on the soil by different species, their different degrees of tolerance of various soil conditions, and the modifications of the effect of the soil factors by differences of physiography and climate, it becomes clear that the actual places in which the individuals of a particular species find themselves, i.e. in which the seeds can germinate and the seedlings become established, must vary very much in their suitability for that species. Unless the combination of conditions approaches the optimum, the plant is more or less handicapped in its life functions. The factor of competition with other species will now play a decisive rôle. A plant may be able to succeed under given combinations of soil and climate if it is growing alone, but not if the conditions enable surrounding plants to grow more vigorously so that they overshadow and tend to smother it. This is well seen in an unweeded garden, where many of the garden plants are soon smothered by weeds if these are not removed.

An experiment which brings out the point has been made on the competition between two species of bedstraw, *Galium saxatile* and *G. sylvestre*, grown together on different types of soil. The former species can tolerate and flourish on acid soils, but if there is an excess of calcium carbonate, the seedlings grow very slowly, suffer from lime chlorosis, and many of them die. Those which survive, however, eventually recover, grow into perfectly healthy plants, flower, and set seed. *G. sylvestre*, on the other hand, can tolerate large amounts of calcium carbonate in the soil, and this does not interfere

with the rapid growth of the seedlings. Consequently, if the seeds are sown intermixed on calcareous soil, the slowly growing and sickly seedlings of *G. saxatile* are overshadowed and killed by the flourishing plants of *G. sylvestre*, even though a few of the former would have survived and grown into healthy plants if the latter species had been absent.

Thus the fact, which we observe in nature, that *G. saxatile* is confined to non-calcareous soils is explained by the fact that it is handicapped, though it does not necessarily die, on calcareous soils, and any seedling starting growth on such soils will be killed by the competition of species which are not so handicapped. Similar experiments will help to determine the causes of the distribution of other species, even though the experimenter may be unable to proceed to the investigation of the physiological causes of the actual effect of the soil on the species, a more difficult problem.

Estimation of Calcium Carbonate Content.—It will be clear from the foregoing discussions that one of the leading chemical characters of soil which has a great effect on vegetation is the *soil reaction*, i.e. the degree of "active" acidity or alkalinity. Soil reaction so often depends on the amount of calcium carbonate present, that some estimation of this is most useful, though this is not of course a direct measure of the reaction as such.

A rough method of estimating the amount of carbonate present, viz. simply pouring a few drops of dilute hydrochloric acid on the soil to be tested has already been mentioned (p. 78, *n.*), Though this method scarcely makes possible a judgment as to the percentage present, yet it does give very useful information as to the degree in which the soil may be described as calcareous, and also as to the distribution of the calcium carbonate. It has also the great advantage that very numerous tests can be made in a short time. If possible, a few different samples of soil giving characteristic results with this test should be collected for exact quantitative determination

of total carbonates, of calcium, and of the other bases, whose relative proportions, as we have seen, may be important.[1]

The behaviour of the soil under each test with HCl should be carefully scrutinised. If the soil contains comparatively large particles of calcium carbonate, the bubbles will be local but vigorously evolved. It must be remembered that such large particles are less effective in neutralising acidity than a much larger number of much smaller scattered particles whose *aggregate surface* is much greater, leading to a general effervescence throughout the soil reached by the acid. A distinction of this sort cannot be made in a soil sample pounded and mixed for a laboratory analysis. Great local differences may often be observed in the carbonate distribution, both from place to place and especially from the soil surface downwards, owing to the progressive leaching of the surface layers by carbonated rain water. If these can be correlated with the distribution of the root systems of different plants, valuable results may be obtained.

Estimation of Soil Reaction.—Direct measurements of the degree of acidity or alkalinity, or rather of the hydrogen ion concentration of the soil solution, can be made colorimetrically by the use of different *indicators*, as they are called, which change colour according to the concentration of free hydrogen ions in a solution. Litmus paper is an indicator of this sort, but it is not sensitive enough for soil work, and has other disadvantages, though it will distinguish quite well between very acid and very alkaline waters or soil solutions. By the use of a series of colour indicators, which can be carried in the field, a very fair quantitative estimation can be made on the spot. But the work can be done more conveniently and more accurately at home if small soil samples are collected. In any case it is unwise to attempt the use of indicators in the field if much other ecological observation is undertaken on the same trip.[2]

[1] See Appendix, p. 212.

[2] Compare the remarks on pp. 85–6. Details as to the use of colour indicators are given in the Appendix, p. 208.

CHAPTER XIII

BIOTIC FACTORS. NATURE AND INTERACTION OF ECOLOGICAL FACTORS. THE HABITAT AND SUCCESSION

BIOTIC FACTORS.

THE biotic[1] factors of the habitat are those which depend directly on the action of living organisms on the vegetation. It is obvious at once that here we are involved in a logical difficulty, for the plants included in any community may, as we have seen, have a profound effect upon one another, just as the individuals of a human community have such an effect. In order to get a practicable working definition it would seem we must exclude the mutual effects of members of the community, and apply the conception of biotic factors of the habitat, i.e. of the community habitat, only to the action of organisms which cannot be regarded as part of the community. But then we are confronted with the question of what is to be regarded as "part" of the community. The soil bacteria? Earthworms and other soil animals? Parasitic fungi? The snails and insects that live on the plants or in the soil, the birds that live in the trees and may play an important part either in destroying or in distributing fruits or seeds, or in doing both? Directly we put such questions we begin to realise how closely interwoven is the web of nature, and how artificial our distinctions and classifications in reality are.

The most natural conception that has been suggested is

[1] Greek *βιωτικός*, pertaining to life (*βίος*).

that which regards the whole complex of organisms—both animals and plants—naturally living together as a sociological unit, the life of which must be considered and studied as a whole. If we extend this conception to its logical limit we must include in the sociological unit not only soil algæ, bacteria, and earthworms, not only insects and parasitic fungi, but rabbits, mice and other rodents. In the semi-natural pasture communities, which are maintained in the condition of pasture by grazing, we must include the sheep or cattle which are regularly pastured upon it, and which, as we have seen, are the chief factor which keeps the plant community in equilibrium. Thus no sharp line can be drawn between organisms which must be regarded as parts of the community and organisms which act as "biotic factors." The plants themselves are also, of course, "biotic factors" in determining the structure and development of the community—they help to determine the fate of their fellows and their own fate too.

For practical purposes it is necessary to regard separately and to study separately as a "biotic factor" any collection or group of animals which have marked effects upon the plants, whether we include them in the wider concept of the community or not.

The ways in which the effects of such animals can be studied are very various. The true field naturalist by acute observation alone can learn a good deal about them qualitatively, but he is seldom able to tell us exactly how much influence they have, especially where a number of different animals are acting together. To obtain such knowledge it is necessary to make exact experiments, by excluding a given animal or type of animal from a portion of the plant community.

Small vertebrates can be kept out of a small plot by enclosing it with a wire netting fence of suitable mesh. One-inch netting will keep out rabbits, while netting of ¼-inch mesh is necessary to exclude mice, and the wire must in both cases be sunk well into the soil. To exclude rabbits in an area

where they are very numerous the buried edge of the netting should be turned outwards at a depth of 6 inches for another 6 inches, so that individuals burrowing just outside the fence with the object of getting into the enclosure will find netting below as well as in front of them. Rabbits will only burrow in this way where there is a severe shortage of food, and the vegetation protected by the wires therefore tempting. The height of the wire above the ground-level should be 3 feet for rabbits, 12 inches for mice. Mice, however, sometimes climb fences of this height. They can be excluded by vertically placed sheet-iron plates or by *covering* the enclosure with ¼-inch wire, which also keeps out birds.

The invertebrates are of course much more difficult to exclude, especially those, such as slugs and snails, which live in or wander through the soil instead of merely traversing its surface. Wire gauze can sometimes be used with advantage for short periods, but this cuts down illumination and prevents the entrance of seeds and fruits into the protected plot. The methods of preventing the access of invertebrates must be left to the ingenuity of workers according to the particular animals to be excluded and the particular conditions of the experiment.[1]

Animals may work in diverse directions: they may eat and damage vegetation so as to cause the replacement of one community by a totally different one, and they may act as pollen or seed distributors, as well as affecting plants in many other ways, altering the soil, for instance, by manuring, loosening or compacting it.

There is good evidence that the regeneration of the grasses

[1] The student is strongly advised to refer to the records of work that has been done with the help of methods of excluding animals, particularly (**33**) Farrow (II, 1916; III, 1917) for rabbits and (**56, 57**) Watt (1919, 1923) for mice, birds and invertebrates. These papers not only give valuable practical details of methods, but will also enlighten the student on the interest and value of the results that can be reached.

and other useful grazing plants of the American cattle ranges in some of the Western States is promoted by the trampling of cattle after the seeds are ripe. It has often been stated that the presence of swine in English beechwoods was necessary for their regeneration from seed. Although the pigs feed on the mast, they are supposed to favour regeneration by trampling some of it into the soil and thus enabling the seeds to germinate; and this may very well be true. It has also been recently suggested that pigs are likely to be of use to the beech by eating various enemies of the seed and seedling, such as mice and slugs. There is abundant evidence that the destruction of carnivorous birds (hawks, jays, etc.) and small animals (stoats, weasels, etc.) by gamekeepers handicaps or destroys the chances of tree regeneration in many of our woods, because the rabbits and mice which are part of their natural prey multiply in their absence and destroy the seeds and seedlings of the trees, especially oak and beech. Thus an interference with the balance of the animal population may alter the relation between one part of it and the dominants of the plant community, and eventually result in the disappearance of the latter.

These are only a few of the cases in which such relations have been shown to be of first importance, but they may serve to illustrate the far-reaching effects that animals may have upon plants. It is much to be desired that field naturalists whose main interest is in animals should co-operate with plant ecologists in the studies necessary to elucidate such relations as those described and others which certainly exist, many of them probably still unsuspected.

Nature and Interaction of Ecological Factors.

In studying the different factors of the habitat and estimating their combined effect on the vegetation, certain principles must always be borne in mind.

The first principal, already alluded to (p. 131), is that the forces which can actually affect plants are limited in

number and nature by the constitution of the plant itself—in the case of the ordinary rooted land plant by those features which are common to all such plants, and also by those peculiar to the species. Apart from "gross" factors, like damage or destruction by wind, frost, fires, grazing animals, insects, parasitic fungi, and the like, when we speak of a "factor" of the habitat such as rainfall, water content of soil, or the kinds and amount of salts present, we must remember that these can only be effective in a limited number of specific ways—ultimately reducible to water, containing various free ions capable of absorption by, or otherwise affecting, the roots, available light falling on the leaves, evaporating power of the air, and temperture. The term "factor" is in fact used in ecology for any substance, force, or condition affecting the vegetation directly or indirectly in such a way as to differentiate it from other vegetation, and the so-called "factors" have always to be ultimately interpreted in terms of the mechanical, physical and chemical processes directly concerned in the life of the plant.

In regard to the water turnover of the plant, a reduced evaporating power of the air means that the roots will make a smaller demand for water on the soil, so that in a region with constantly humid air the same species can grow on soil which has a lower water supply. Direct evaporation from the soil itself in a humid climate will also, of course, be much less, so that the soil will maintain an adequate water supply with a much lower rainfall than would be necessary in a hot climate. Thus a sandy soil in the West of England, where both rainfall and air humidity are high, will support a more moisture-loving vegetation than in the Eastern Counties. Again, in the East of England most soils, owing to the comparatively high air humidity, will support a more luxuriant vegetation, with a rainfall of 20 inches, than in a continental climate, where the same soils with the same rainfall would produce only a dry grassland. Similar relations of air and soil moisture may be

seen on a smaller scale wherever the physiographical features produce sharp difference of "local climate," as in steep ravines and on exposed ridges.

Replacement of One Ecological Factor by Another. Such cases as those just mentioned illustrate what has been called the replacement (or compensation) of one factor by another. Thus many of the same species occur on the south exposures of hills with dry shallow soils in Western and Western-Central Europe as on various soils and exposures in the drier Mediterranean climate. Here the local physiographic and edaphic factors replace the general climatic factors of the Mediterranean region. Inversely, steep northern exposures (cf. p. 142) and deep ravines in the Mediterranean region often bear a distinctly northern vegetation. Beechwoods in the damp climate of England are practically confined to relatively dry permeable soils (chalk and sand); in the much drier climate of Continental Europe they occur on a greater variety of soils.

Sometimes biotic factors replace climatic ones. On the Swiss Alps in Canton Valais a certain heavily pastured grass and herb community on a dry south exposure showed a strikingly similar vegetation with the same "life forms" and the same "aspects" as the Hungarian "pusta"—the heavy pasturing (reinforced by the "local climate" due to south exposure) bringing about a similar set of conditions to the continental climate of Central Hungary. And so in many other instances.

Limiting Factors.—The second principle is what has been called the law of "limiting factors," which is of great importance in ecology. When the co-operation of two or more "factors," e.g. definite quantities of different substances, temperatures within certain limits, a certain degree of illumination, etc., are required for the maintenance of any process, then, if one of the "factors" is absent, the process stops whether the others are present or not. Similarly, if the *rapidity* of a process varies with the quantity or degree

of several different "factors" acting together, the reduction of any one of them will reduce the rate of the process, even though the others are present in sufficient quantity or degree, or in excess.

Thus the necessary mineral salts may be present in the soil, temperature and light may be favourable; but if water is absent the plant cannot grow, and if minimal amounts are present it can only grow very slowly, as in a desert. Again, if the temperature remains below freezing-point, plants cannot grow, though all the other factors may be present. And as the temperature rises above freezing-point growth will steadily increase up to a certain point if the other factors are maintained in adequate degree. It may, for instance, be checked by the water factor, the water supply in the soil being adequate to maintain the slow growth which can take place at 5° C., but inadequate to the more rapid growth which would take place at 15° C. or 25° C. if sufficient water were available. The rise in temperature will also tend to decrease the water supply in the soil by increased evaporation, both directly through the soil and also through the plants, and this last effect (increase of transpiration) may render the plant unable to cover its water loss by absorption from the soil. And so with the other necessary factors, carbon dioxide, light, and mineral salts capable of absorption by the plant and containing the necessary elements. The factor which is present in so low a quantity or degree that it limits growth or some other life process is called the *limiting factor.*

The Habitat and Succession.—A final point about the habitat should always be kept in view—the fact that it may *change* progressively, both along with the vegetation and more or less independently also. This point has already been considered in Chapter IV, where we saw that succession or development of vegetation from a starting-point on bare ground was normally accompanied by a gradual increase of humus, and that this increase in its turn progressively fitted the ground for different kinds of vegetation until a

climax was reached. On all the more favourable soils this climax tends to be determined by climate (climatic climax), and to represent the highest (most complex) type of vegetation that can exist in the general climatic conditions. We have seen in Chapter XI how humus comes to be of such great importance in "improving" the soil, provided there is a quick "turnover," and thus in helping to provide the most favourable conditions for vegetation. If these favourable conditions are maintained indefinitely the climatic climax will be correspondingly maintained.

Accumulation of Acid Humus.—Other factors may, however, come into play. In a cool humid climate, such as we get on and near the western coasts of the British Islands, the humus does not disintegrate so rapidly as it is formed, and thus tends to accumulate as raw humus. In the wetter places this results in the formation of peat, and we get mosses and moors instead of forest. This is most marked over soils poor in lime and in mineral bases generally,[1] because the presence of basic ions tends to promote the growth and activity of soil organisms which disintegrate the humus and provide food for the higher plants (other than moss and moor plants). But under cool and extremely moist conditions, especially if the soil is badly aerated, raw humus and peat may form even over limestone itself. Here we have good examples of the replacement of factors already described. A cool moist climate, local excess of soil water, poverty in mineral salts, and poor aeration, are all factors tending in one direction, and may to a considerable extent replace one another.

Leaching.—Another factor tending to alter the habitat in the same direction, and having a considerable effect in the British Isles, is the leaching or washing out of soluble

[1] It is, however, held by some workers that a preponderance of potassium and sodium over magnesium and calcium in the water favours the growth of moor and moss plants as well as a corresponding aquatic vegetation.

mineral salts. Different salts are soluble to very various degrees. Sodium chloride and the other haloid salts left in maritime soils wash out the most readily, and thus alter the habitat presented by these soils when they are no longer supplied with fresh salts. Of the salts present in ordinary soils calcium carbonate is most readily leached out by water containing much carbon dioxide, while magnesium and potassium salts dissolve much less quickly. The impoverishment of the surface layers of soil in calcium carbonate and, to a less degree, in other bases will lead to "acid conditions" and to the establishment of acid-tolerant plants, and may gradually change the whole character of the vegetation. It is believed that much of our semi-natural vegetation has been, and is being, steadily altered in this way. In wet regions leaching will clearly assist peat formation, in drier ones it will slow down the turnover of humus and thus tend to the accumulation of raw humus, for instance, on a forest floor; and this may help, along with other factors, to prevent the regeneration of the forest, or lead to the replacement of one species of dominant tree by another.

Flushes.—Where the surface soil is constantly supplied with fresh bases these changes will not occur. The "flushes," as they are called, often seen in grassland and in woodland on sloping ground are areas irrigated by waters from springs or from the run-off of rainfall on the ground above. If these waters contain mineral salts as well as free oxygen in solution, the flush will bear a distinctive vegetation of various grasses, herbs, etc., often fresh green in colour in the midst of a brownish acid-tolerant vegetation of the general hillside. In other cases an "acid flush" with acid-tolerant plants in the midst of a vegetation of plants growing only where they can obtain a good supply of bases may be formed by water draining from a moss or moor.

PART V

ECOLOGICAL WORK IN SCHOOLS

CHAPTER XIV

ECOLOGY AND "NATURE STUDY"

THE author is convinced of the great educational value of ecology in schools, and it is hoped that the foregoing chapters will enable masters and mistresses to get some clear idea of the possibilities of the subject and of the ways in which it can be approached and developed *in the field*. It is unnecessary to say that this book is not intended—is indeed obviously quite unsuitable—as a school class-book. Much of the work suggested could not possibly be undertaken by school classes, and the book is written for the adult mind, though it is hoped that most of it at least will be intelligible to those who have had no very detailed training in botany.

This chapter and the next contain specific suggestions to teachers—put forward with the diffidence due from one who has no first-hand experience of school teaching—as to the ways in which ecology can be used in schools. Opportunities for such work vary widely between different schools. In a city school with no school garden it is practically impossible to carry on any systematic work in the subject. The most that could be done would be to try to arouse some interest in vegetation on country excursions, but without some previous acquaintance with the species of plants even this would probably not be very profitable or successful. Botany, of course, can be taught—after a fashion—in a city school, but scarcely ecology, which must

depend on first-hand acquaintance with plants in the field and garden.

In a school placed in a country town or in the countryside itself the case is quite otherwise, but any considerable development of the subject must depend on two other factors —the whole-hearted sympathy of the headmaster or mistress and the aptitude and enthusiasm for such work of the actual teacher. In the absence of the first it would be difficult or impossible to find the necessary time and opportunities, and without the second it is most unlikely that the pupils would ever become sufficiently interested to make the thing worth while. The suggestions and hints which follow can therefore be made full use of only by those who are fortunately situated in these respects.

At the outset it must be borne in mind that ecology, in the wide sense explained in Chapter I—and it is, of course, in this sense that its school value is to be considered—is essentially *a way of looking at plants. It should never be divorced in teaching from the actual study of the plants themselves, of their structure, development and functions.* But the relative importance of the various characters presented by plants can be interpreted from the ecological point of view. In other words, the features of plants can be looked upon as of importance in relation to their actual life in the field as members of plant communities rather than from other points of view.

The Wrong Way to Teach.—In saying this we are as far as possible from wishing to defend or excuse such practices, still too common, as describing in the classroom so-called "adaptations" of plants; of teaching that a whole series of structural features are "protective," without attempting to find out what they "protect" against, or whether it is really effective against particular inimical factors; of giving the impression that every flower is a perfect pollination mechanism; of classifying plants into xerophytes, mesophytes and hydrophytes, and leaving it at that; above all, of finding a "use" for every

part and feature of a plant. This whole method of teaching is most mischievous. It quite literally corrupts (scientifically) the minds of school-children, by substituting facile and largely inaccurate generalisations for observation of nature and sound induction. It is "all too human" a tendency to find a "use" for everything, to put things into mental pigeon holes and leave them there as finished with. It should be the first function of school science teaching to correct such bad mental habits. We need not, therefore, deny that many things *have* "uses," i.e. that they may fit well—sometimes marvellously well—into schemes or "mechanisms" which benefit living organisms, even that the process of evolution largely consists in the organisation of such schemes and mechanisms; nor need we deny that pigeon holes are admirable temporary conveniences, provided that pigeon holing is not taken as an end in itself.

But what we want, to start with, is observation of the facts of nature as they are, and then to go on to find out as far as possible how they came to be so. Happily, such inquiry is also a natural human impulse, though it may very easily be stultified or even destroyed by false methods of teaching and mental laziness.

In a school where the opportunities do exist and the conditions are favourable, it is most desirable to begin early, and to continue throughout the school course, open-air work in which ecology can play its part.

"Nature Study"—The Foundation of Ecology.—Ecology *is* nature study *par excellence*, and although the work in the lower forms of many secondary schools that goes under that name is not exactly ecology, it can very well be used to form a good foundation.

There is no better starting-point than the germination of the seed and the structure and growth of seedlings. This work can be adapted to any age, and the whole of it can be followed and observed by the children, who can grow the seedlings of different plants for themselves in pots and boxes,

and in the garden if there is one available. They can learn the origin and history of the different structures produced, and, by the simplest experiments, some, if not all, of the necessary conditions for germination and subsequent growth.[1] They can see how widely the seeds and seedlings of different kinds of plants differ from one another, and yet that there is a general plan of structure common to them all.

Here may be introduced some early lessons on soil, even simpler and more elementary than the work described in Russell's book, if the children are too young for that. It is most desirable to keep the study of the soil in the closest relation to the study of the plant from the very beginning. The differences between garden soil and natural soils can be illustrated by actual examples from the neighbourhood. A first study of seedlings and soil might very well occupy one term. Let us say it is the second winter term, a very suitable time for such work.

If the course begins in the autumn a start may be made with fruits and seeds. As many as possible should be collected from every source, and the different plans of structure examined and drawn. When possible, the development of fruit from the flower should be followed: it does not matter if no study has yet been made of the flower itself. The swelling or change of the carpels can quite well be taken as a starting-point. The work on fruits and seeds may be continued after Christmas, and the germination of seeds only begun in February or March, at first indoors, and continued after Easter, when seedlings are springing up vigorously everywhere.

In the summer term it will be natural to tackle older plants

[1] The quantitative estimation of the water present in the seed, the minimal temperature for germination and growth, and the oxygen supply necessary, are of course suitable only for much older pupils. But the necessity of these factors can be clearly established by the quite young children with a little ingenuity on the part of the teacher. "The little baby plant sends out its tiny roots to search for water," and all such sentimentality should be rigorously avoided. It is alien from science and brings the subject into contempt with natural healthy minded children.

and flowers. The particular work must now depend very much not only on the age of the pupils, but on the particular school and its opportunities. For instance, if there are facilities for indoor laboratory work, and neither garden nor field work can be made a feature, simple experiments on growth, perhaps also on transpiration and photosynthesis may be carried out, and at the same time different types of life form (see Appendix, p. 197) examined and compared. To this the structure and functions of the flower and the comparison of a *limited number* of different types of flower may be added. These topics will probably amply fill the summer term.

If, on the other hand, the school garden is a feature of the school, and the children are allowed to work in it, they can begin to get an invaluable first-hand acquaintance with many things : cultivation of the soil ; growth of different life forms from seed, from rootstocks, from corms or bulbs ; effect of different kinds of weather on different plants ; weeds and their life forms, e.g. the difference between the comparatively harmless annual weeds, like shepherd's purse and groundsel, which in moist weather can easily be pulled up with the finger and thumb, and the pestilent weeds with deep-seated, quickly growing rhizomes or suboles, like field bindweed, twitch and the like. All these things afford ample material for drawing in the classroom, and thus fixing in the memory.

It is, perhaps, unnecessary to say that the ideal of a school garden is not a " tidy " garden devoted to well-kept flowers and crops of vegetables, but an outdoor laboratory for studying the growth of different kinds of plants and the conditions under which they succeed or fail. Certain beds may be kept for the production of flowers and vegetables, and in these the lessons learned in the " working " beds may be applied. But in the latter the children should by no means be forbidden, they should be encouraged, to dig up seedlings and older plants " to see how they are getting on," to look at the nature and development of the underground parts, the

depth at which these grow, and so on. It should be a point of honour to know exactly what the underground parts of every kind of plant grown and of every weed is like, and the kinds of plants grown should be chosen largely to illustrate different life forms. They should be sufficient in number for this purpose, but not too many.

Finally, if half-day excursions to the open country are possible—say once a week—these may be made the pivot of the term's work. Following on the general knowledge of seedlings acquired during the spring, one of the first excursions may be devoted to marking with stakes (inconspicuous if the place is frequented) or otherwise, sets of seedlings that are met with on waysides, hedgebanks, the edges of woods, and in arable fields, with a view to observing them week by week and noting what happens to them. Some will die and disappear from causes not easy to discover, some will be smothered by the growth of neighbouring plants, or will starve each other of light, grow up long and spindly, and finally die. Some may be attacked and crippled or destroyed by minute insects or by parasitic fungi, others trampled down or eaten off by browsing or nibbling animals. Others, again, may dry up from want of soil water. But some will grow into adult plants, and interest will be aroused and maintained as to what plants they will grow into. These can be watched week by week, and their progress noted, until the time comes when the plants can be identified.

During the first few weeks the discovery of seedlings that can be marked, and the observations upon them, will occupy a large part of the time available. Where there is an abundant crop, specimens should be carefully dug up and taken back to school in tin boxes, to be drawn to scale, the earth having been carefully washed from their roots; and so from week to week if the seedlings have grown enough. As time goes on, so many will have disappeared, and the ones that remain will be so well known, that less and less time will be required for following their progress.

Meanwhile other matters can be attended to. A certain number of perennial plants can be chosen for study. The particular species chosen must of course depend on what grows in the neighbourhood. They should not be too numerous (perhaps half a dozen), and they should all be common plants, so far as possible characteristic of different communities, e.g. a woodland plant like dog's mercury, stitchwort, or wood violet, a heath plant like the ling itself, a wayside plant like silverweed or a species of plantain, one or two pasture plants, including a dominant grass, and so on. To these may be added two or three annuals, preferably those whose development has been followed from the seedling.

In a mainly agricultural region, where most of the land is under the plough, at least half the plants may be chosen from among arable weeds, and the balance from hedgebank and wayside plants. But if any areas of comparatively natural vegetation exist in the neighbourhood, such as heath, common or down, then dominant or characteristic plants from these should certainly be included in the list.

Everything possible should be ascertained about the species chosen, including as many as may be of the following points: life-form, i.e. mode of perennation, depth at which the roots are mainly developed, general structure of shoot system, vegetative propagation; any soil preferences or other habitat preferences that may be observed, time of coming into flower, duration of flower, structure of flower, mode of pollination,[1] whether seed is set and ripened, and if so how much; relations to other plants (competition, etc.). This will be a sufficient programme for the summer term, and if the children are very young, it will have to be considerably simplified, for

[1] This is by no means always easy to determine. The simple experiment of tying a muslin bag over the flowers will show whether large insects are necessary, but small insects (e.g. Thrips) can crawl through most muslins. The muslin may also, in a wet season, interfere with evaporation sufficiently to cause the flower to rot. Nevertheless the attempt should be made.

instance, by cutting down the number of species chosen for study, and also the points studied. But the *kind* of work required is important, for the kind described draws out and trains the powers of observation, raises all sorts of interesting questions, some of which can be answered at once, while others may be answered in later years. At the same time such work is undoubtedly the best foundation for the future. It need not be said that more work than can be properly carried out should not be undertaken.

It may again be emphasised that the suggested work in the laboratory, garden and field are intended as *alternatives*. If it should happen that any of the three would be possible, the garden is probably to be preferred as the pivot of the work during the first year, and, after the garden, the field is probably to be preferred to the laboratory, because either garden or field brings the children from the outset into touch with plants as they grow. Either garden or field work should be supplemented by classroom work for drawing, recording observations in permanent form, and discussing results. So far as may be both individual emulation and also co-operation should be used to stimulate work, and the putting of questions to nature should go hand in hand with observation.

The age at which nature study work is begun must, of course, determine the fullness with which such a programme as that suggested for the first year could be carried out. If the average age of the pupils is eight or nine, it would clearly have to be restricted and simplified; with bright children of ten or eleven it might be followed fairly closely. In the former case a second year's work might follow the lines of the first with fuller material, or the field or laboratory might be used instead of the garden. In the latter case fresh material may be introduced. For instance, trees instead of herbs could be taken as the main subject of the second year's work. The fruits of available trees, especially the commoner British ones—oak, beech, ash, birch, pine,

with sycamore and any others accessible—could be studied in the autumn, and the opportunity of early autumn walks taken to observe the natural dispersal (or non-dispersal [1]) of those fruits (notably oak, beech and sycamore) which are shed at that time. This work could be supplemented by observation of the method of leaf fall and of the winter condition of the trees—the general shape of the different kinds, the form, colour and protection of the twigs and winter buds, the bark of the trunk, etc. The children could be asked to draw some of the kinds of tree from memory at the beginning or early in the course, and the results would at once reveal how far they had already observed their forms and could express them on paper. The attempts would serve as good starting-points for more deliberate observation.

In the spring, seeds which had been collected and kept (perhaps under different conditions, e.g. moist and dry, well aerated and closely packed) could be put to germinate and the results observed. The process of germination and growth of the different seedlings could then be followed. Afterwards the best seedlings could be planted out in the garden.

In the late spring and summer the leafing of the different trees should be observed, the shade they cast and the shade the seedlings and young trees can endure if possible compared. The structure of the flowers and their mode of pollination should be looked into.

If woods are accessible, some of the ground species which grow in shade or half-shade can be taken up for study on the lines suggested above, in addition to the species chosen for the first year's work. In this way the beginnings of a study of woodlands can be made.

[1] Do the shed fruits of these trees really contain fertile seed? Beech mast, for instance, often does not. Do they get far from the parent tree? If so, how?

CHAPTER XV

DEVELOPMENT OF ECOLOGICAL WORK

IT is probable that two years of nature study devoted, or mainly devoted, to plants are enough. It is now customary in many schools to break off all biological teaching at the age of eleven or twelve, and to teach only Chemistry and Physics or "general science," until, at a later age, say sixteen, some of the pupils "specialise" in Science. It is not, of course, part of the purpose of this chapter to discuss the merits and demerits of this system. But in the author's view it is educationally bad to stop the teaching of biology at so early an age. While admitting the claims of Chemistry and Physics to the larger share of the time devoted to science from twelve to sixteen, he is strongly of opinion that some effort should be made to keep alive during these years the biological interests that have been aroused by nature study. Biology, in some form, should be regarded as of primary importance, if only because we ourselves happen to be living beings. The author thinks that at least one teaching period a week should be devoted to biology throughout the school years, and that this should be reinforced by the establishment in country schools of a Field Club or Natural History Society, and by the encouragement of voluntary work at some branch of the subject.

It is by no means necessary, of course, that ecology should be the pivot on which this "continuation biology" should turn. In city schools it cannot be; and besides, there are other ways of treating biology, particularly those leading up directly to its bearing on human life, which have the most serious claims. On the other hand, there are many country

schools where ecology is certainly suitable, and if it is properly taught it must stand very high in educational value. We may now, therefore, consider the lines along which it may be developed, either as a regular school subject, or as voluntary work of the pupils and teacher. The most desirable thing is that it should be partly one and partly the other, and the adjustment of the two spheres should not be beyond the powers of an enthusiastic teacher, supported by the sympathy of the head of the school. Possible lines of work will be outlined in quite general terms, since it is clear that the detailed adaptation to special circumstances must be made by the teacher.

The earlier nature study on the lines suggested will have taught the facts of the life history of a limited number of species pretty thoroughly, and should have laid the foundation of the habit of looking at plants in the right way. The work may now be developed either on intensive or on extensive lines. The immediate advantage of intensive work is that it does not require a wide and accurate knowledge of the flora. If the work is confined to small plots of ground, all the species met with will soon be well known and easily recognised at all stages of growth, and a fairly exhaustive knowledge of their life histories obtained. This sort of work is very attractive to some minds, and it is excellent training in thoroughness and careful attention to detail. But it does not appeal to all, and a more superficial acquaintance with a much wider range of species and of vegetation, which may be accurate enough as far as it goes, is also very good training, though better for rather older minds. Extensive work is only practicable, of course, when there is freedom to move about the country-side. The ideal thing, no doubt, is to begin with the sort of work suggested as nature study, to go on with intensive quantitative work, and later to widen the range by extensive observation.[1] This course may very well be possible

[1] The thesis laid down in Chapter VII, that extensive survey is the best preparation for intensive work, applies to adults freshly approaching ecology, not to the training of children.

in the case of a few of the keenest pupils at a school where ecological work is an established feature of the curriculum.

An important consideration, which must again be emphasised here, is that school ecology should always be regarded as a means of approach to Botany, the object being to learn about plants rather than to practise certain methods of work. A very great part of Botany can be approached in this way, though much of the more advanced work must eventually be carried out in the laboratory.

The Use of the Quadrat.—The different uses of quadrats in the study of vegetation have been described in Chapter IX. For intensive work at schools the quadrat is invaluable, and particularly the permanent or semi-permanent quadrat which is charted or listed at intervals.

Garden Quadrats.—If there is a school garden, a certain number of quadrats on bare soil should be laid out and made permanent with corner pegs and durable laths or rods marked in small divisions (decimetres[1] or 6-inch intervals). If there are marked differences of soil in the garden, or one part is always wetter than another, or some parts are shaded and others exposed, one or more quadrats should be laid out in each. It is best to lay out the permanent quadrats in the winter when the soil is quite bare. Access to each quadrat must be provided for. It has to be remembered that approach must be possible in all states of the soil. A quadrat cannot be accurately charted unless the observer can get his eyes close to every part of the surface, so that it becomes necessary to kneel or even lie beside it. Strips of waterproof should be provided, or the clothes will be likely to be made very dirty, especially if the soil is at all heavy.

The garden quadrats should be first charted as soon as the first crop of seedlings appears, and thereafter at fort-

[1] If any considerable number of the pupils are likely to specialise in Science, it is an advantage to use the metric system from the beginning. The boundary laths of the square metre may then be marked permanently in decimetres (red) and centimetres (black) with good oil paint.

nightly or monthly intervals throughout the summer term, and again immediately after the summer holidays. The seedlings will, of course, be mainly "weed" seedlings, though some of the more easily dispersed garden plants may appear. It will be impossible at first to distinguish the seedlings of different plants, though different types of cotyledons will be noticed at once. Consequently symbols must be decided upon for the different unknown seedlings, preferably crosses, dots, circles, etc., and these must be at once recorded, with a short description of each, on the space left on the chart card (see p. 109). Later, fresh symbols will have to be added as new seedlings appear.

Attention should be paid to the remarks on p. 111 about the size of the symbol being proportionate on the chart to the space occupied by the plant on the ground. If the seedlings come up very numerous and thick it will be impossible to chart the whole quadrat properly on the 1 : 10 scale. In that case a part of the quadrat only (say one quarter or even less) should be charted, strings or tapes being run to make the two internal boundaries of the portion to be charted. A careful note must be made of the scale actually employed and of the part charted. Always use the same size of blank chart (a square decimetre is the best), and see that the symbols are not unduly crowded by taking care to chart an area of suitable size. If only a portion of the square metre can be charted at first, yet later on, when many of the seedlings have disappeared owing to various causes, it is probable that the whole square metre can be charted on the 1 : 10 scale.

As the seedlings grow the species to which they belong will gradually be identified, and in this way a very full knowledge of the garden weeds, their rate and mode of development, is acquired. As soon as the seedlings denoted by a certain symbol on the first charts are identified as a particular species the initial letter (see p. 104) of its name should be substituted for the symbol of the earlier charts, and the new symbol (letter) with the name it denotes written in the space below the chart.

Every chart must be designated by a letter or number or both [1] and carefully dated. The charting should be done very neatly in pencil, and inked in as soon as possible after completion. All these charts must be carefully kept in a safe place, always available for reference. Comparison of the successive charts of the different quadrats from year to year will furnish most instructive data for drawing conclusions of various kinds.

It will certainly be found that the different quadrats will show at least somewhat different plant populations, though many of them will have several species in common. The differences will partly depend on what seeds were in the soil to start with; they may be related to habitat (soil differences, water, shade, etc.), they may be related to proximity of seed parents, or they may be a matter of chance. All these possible causes of difference will furnish useful points for consideration and further study. Besides the first colonisation, there will be a succession of plants from year to year on the same quadrat. Some species will remain for a long time, others will be very transitory. It is, of course, very much to be desired that all the permanent quadrats should remain undisturbed for as many years as possible. The longer they are left the more instructive they will become. No plants should be pulled up or disturbed in any way. The dead ones must be left to rot where they die. If a quadrat should become the centre of distribution of a pestilent weed which spreads by underground rhizomes or suboles, it may be isolated by digging a narrow deep trench round it, but not so close as to drain the soil of the quadrat.

The interest of permanent quadrat work is very great, and no one who has once become fairly fascinated will readily abandon it. The detailed knowledge of the behaviour of seedlings and older plants that is acquired, and most easily

[1] It is convenient to give every permanent quadrat in the garden a letter, A, B, C, etc., and add a number to the letter on each fortnightly (or monthly) chart. Thus the second chart of the third quadrat will be C2, etc.

acquired, even in one season's work, is astonishing. The effort to chart the quadrat accurately directs the attention towards and fixes it upon details that would very likely be missed altogether with ordinary observation, while the re-observation of the same individual plants at definite intervals gives an extraordinarily close picture of their growth and development. Root systems cannot, of course, be studied on the permanent quadrat itself because the plants must not be disturbed, but examples of the same species from other parts of the garden can be dug up for examination. If desired, the record furnished by the succession of quadrat charts can be completed by series of drawings of the different species represented.

Garden quadrats can, of course, be used for all kinds of purposes besides tracing the succession of plants on the permanent quadrats. For instance, experimental quadrats can be laid out, and various experiments tried upon them—over-watering, protection from rain, various kinds and degrees of shading, various kinds of manuring, determination of the seeds introduced with stable manure or other dung, and so on. If the method of teaching by means of the study of quadrats is found to be successful enough to warrant a wider application—and if the facilities described can be obtained and the necessary time devoted this will probably be the case—experiments of the kind indicated will readily suggest themselves to the experimentally minded teacher.

Field Quadrats and Transects.—It will seldom be possible in school work to make such extensive use of permanent quadrats in the field as in the garden, if only because spots in which they can be usefully laid out with no danger of disturbance are often hard to find. An established plant community may show little change from year to year, so that a quadrat, unless it is treated experimentally, will teach little but its original structure. Charting a temporary quadrat, however, is one of the best ways of finding out the detailed structure at any spot of a close complex community,

such, for instance, as old-established grassland, because every square inch of ground must be examined. Such quadrats are also very useful for listing with a view to ascertaining the occurrence and frequency of different species.

On bare or partially bare soil which is being colonised, or wherever change is going on, permanent or semi-permanent quadrats are useful for studying succession, if they are reasonably secure from disturbance. Permission from a friendly landowner and the goodwill of keepers, shepherds, etc., is very desirable and may be indispensable. The outlines of procedure are just the same as in the garden. The quadrat should be charted at regular intervals, though these need not be so short, because growth and change is rarely so rapid as in the garden. Three charts during the season (say April, June and September) are generally enough, even early in succession and when there are marked seasonal aspects. Often one chart in the year will be enough. But what is necessary in any given case can only be determined on the spot.

Line transects and belt transects (pp. 105–108) are particularly useful at right angles to the direction of the zones in any zoned vegetation. The advantage of a line transect is the rapidity with which it can be made. Thus more than one line transect, if not too long, can easily be made by a party on an afternoon's walk, provided the species present are known beforehand. A long transect can be split up into sections and different members can work at different sections, simultaneously (two at each).

Extensive Work in the Field.—For this, of course, a knowledge of the flora is indispensable. Pupils will soon learn the names of the limited number of species that will be met with as weeds in a garden or on a given small set of quadrats in the field, but the two or three hundred species of flowering plants alone, which will be commonly met with in the various communities of even a limited area of countryside, are quite a different matter. It is doubtful whether it would be possible or desirable to insist on such knowledge

being obtained by all pupils, even in a school where field botany could be made a special feature of the school work. A few would acquire it willingly, but not the majority, and it is more than doubtful if any good purpose would be served by compulsory acquisition of such knowledge. It will therefore be necessary to make any thorough extensive work that may be undertaken voluntary work, carried out by a few of the older and keener pupils.

It is nevertheless very desirable that all school botany should include a certain serious knowledge of the differences between species,[1] though the number of species may be quite limited. This kind of knowledge is probably best and most easily acquired at the outset by the necessity of identifying the plants which appear on garden or field quadrats, or field stations under observation, because so much more interest is centred on them than on specimens brought in from outside. But some regular lessons on the differences between species should also be given, and the empirical knowledge already acquired on the quadrats will be most useful here. It cannot be too strongly insisted that such lessons should begin with the smaller differences, i.e. those between allied species of *one genus,* and *not* with families and classes. The plantains, the buttercups and the speedwells are excellent genera on which to make a start; and only when a firm grip has been obtained on the nature of specific differences should the conceptions of genera, families, and larger groups be taken in hand. This depends on the fact that species (or many of them) are real natural entities, while the higher taxonomic groups merely represent the human effort to classify the species. If taxonomy is taught "from the top," for instance by beginning with the characters of classes or families, it often happens that no real first-hand knowledge of species, i.e. of the things actually classified, is ever obtained; and no one can have any sound or useful

[1] A good flora and illustrations should always be available for reference.

knowledge of systematic botany who does not know species. From the educational point of view, the *number* of species he knows or is able to put into genera or families at any given moment is of relatively minor importance. Once he has got a firm grip of the kind of differences that separate species and the habit of looking at these, he can always easily extend his taxonomic knowledge at will. If he never gets this grip and habit, he can never acquire any sound taxonomic knowledge at all. Furthermore, the power of discriminating small differences in natural objects is a very valuable mental training, of use in every occupation and department of life.

It is therefore suggested, on all grounds, that the identification and discrimination of species should form a recognised part of the teaching in botany immediately following and continuing the "nature study" period.[1] The species chosen should be partly groups of allied species belonging to single genera (*Veronica, Lamium, Ranunculus, Stellaria, Cerastium, Plantago, Poa,* etc.), and partly dominants and other common species of easily accessible plant communities. After a year or two at this kind of work, with frequent opportunities of seeing the species in the field, a good acquaintance with at least forty or fifty species of flowering plants should be easily obtained, and those pupils who have a natural taste for this part of the subject will rapidly widen their knowledge as time goes on.

From the beginning (in the nature study course) different "life forms" (i.e. the vegetative structure of the whole plant) will have been distinguished, and attention directed to the habitats (i.e. the kinds of places in which the species are habitually found). Of course, one life form is by no means

[1] There are few, if any, school floras really good as an aid to this work. Artificial dichotomous keys are not to be recommended, even if they are efficient. They give false notions of actual differences, and emphasise the process of identification at the expense of a real knowledge of specific characters. The best floras are unsuitable for beginners. It is suggested that the making of synopses from the actual plants, at first of the species of a genus where several species can be obtained, later of the genera of a family, would be a valuable class exercise.

confined exclusively to one habitat. But certain correspondences will be noted: for instance, the prevalence of long underground shoots in all kinds of loose or soft soil, whether woodland humus, the wet soil of marshes and watersides, or loose garden soil; the dominance of annuals in ploughland, garden beds, and on bare soil generally; of plants, like the turf-forming grasses, which branch freely from buds close to the surface (either just below or just above) in pastures and on lawns.

With so much knowledge of species and life forms the study of a plant community in the field may be taken up. What the particular community will be must depend mainly on what is readily accessible. A heath or any kind of common land often best fulfils the necessary conditions; woodlands less often, because they are usually private property and are often preserved for game. Marsh and water vegetation is very interesting, but regular study of it presents difficulties and inconveniences. A seaside school within reach of sand dunes and salt marshes has an unrivalled field of work.

The methods of work may be selected from those described in earlier chapters. Here we need only summarise the principal subjects that may be investigated, beginning with those that naturally come first. But it is not necessary, of course, to take them exactly in this order, nor to complete one before beginning another.

1. List of species, as complete as possible, and identification of those not already known.
2. Preliminary attempt to determine the minor plant communities (consociations or societies) present.
3. Vegetation map on a scale suitable to the area and type of vegetation (see Appendix p. 200). This is only worth making if the distribution can be correlated with habitat conditions (of whatever kind), or there is an obvious general invasion or succession proceeding. If the vegetation is substantially uniform over the whole area (apart

of course from local variations not obviously correlated with habitat), there is little point in making a general map. In a diversified agricultural region making crop maps based on the 6-inch Ordnance Survey maps is an interesting and instructive exercise. A series of crop maps, one for each year, will give interesting information on the different systems of agricultural treatment.

4. Quadrat and transect charts. These may be used for getting a closer idea of the structure of the vegetation, but are not always worth while in uniform and stable vegetation. The teacher must use his judgment. If, however, the vegetation is zoned, or succession is clearly proceeding, either generally or locally, transects or quadrats, or both, should certainly be laid down, and the changes followed in successive years.
5. Studies of habitat factors (see Chapters X–XIII), including for instance regular grazing or rabbit attack.
6. Special studies on various questions that may arise in the course of the earlier work, e.g. problems connected with seed dispersal, or effect of fires (regeneration or replacement by other vegetation, etc.).

A study of the kind suggested, carried out on a favourable community and continued for some years, would not only have great educational value, but would also almost certainly contribute sufficiently to our knowledge of ecology to be well worth publication. A tradition of genuine observation of nature will be gradually established in the school, with literally incalculable benefit to many of the pupils, and benefit also to the progress of ecology itself.

If no such detailed study of a particular community is possible, something can be done on half-day excursions to different communities, e.g. different types of common, down, woodland, mountain-side, fen, or seashore. Though the knowledge obtained will necessarily be more superficial,

it should *not* be confined to making lists of the species encountered. It will, of course, entail a wider knowledge of species, and if the foundations of species discrimination have been well laid, will arouse considerable interest. The different sets of life forms should be noted, and characteristic specimens and soil samples brought home. Line transects and list quadrats can be made in a short time, and successive visits will eventually amass considerable knowledge of the various communities and their successions and habitats. Even if regular work on a single community is possible, it is good to intersperse it with visits of this sort to other types of vegetation.

The Groups of Non-Vascular Plants.—In what has been said above no specific reference has been made to the lower plants—mosses, liverworts, lichens, algæ and fungi—which are often important elements in communities dominated by vascular plants, and not seldom form well-marked minor communities of their own. The lower plants are, in fact, too often neglected by working ecologists, usually from ignorance of their species, though there is, in recent years, considerable improvement in this respect. It is no light task to obtain even a moderate working knowledge of all these groups. But something can and should be done by the teacher who undertakes to conduct ecological work in the field. A beginning may be made with the commonest mosses and lichens, the names of which can be ascertained without too much labour with the help of the standard handbooks on these groups. Gradually the forms most commonly met with in the plant communities taken up for study will become well known to teacher and pupils. The British specialists on these groups will always give ready and courteous help to serious students in naming the rarer and more difficult species. As time goes on it is very likely that the older pupils will come to take special interest in different groups, and may become "authorities" to whom unknown specimens will be brought.

The non-vascular plants should certainly not be neglected

altogether, not only on account of their intrinsic interest, but because they are often important pioneers in succession. Certain species, also, are of diagnostic value as constant members of particular communities of higher plants.

Relation of Ecology to Other Botanical Work in Schools.—It will have become clear from what has been said that, where the opportunities exist, ecology in the widest sense, including ecological work in the garden (rather than "gardening" in the ordinary meaning), may well be made the pivot of a regular botanical training. As was stated at the outset (Chapter I), ecology in the wide sense is a means of approach to a large part, and that the most important part, from the point of view of the school, of the science of plants.

The most thoroughgoing way in which this means of approach can be employed is to use the plants of some neighbouring community or communities, as has actually been done in a boys' school in the North of England (Price Evans, 1920), as the basis of practically the whole of the school work in botany. If these wild plants are supplemented by certain almost indispensable types, such as the broad bean, the French bean, the gourd or marrow, some common cereal such as wheat, and perhaps the castor-oil plant, which can very easily be grown in the garden, hardly any material from outside will be required. The elements of morphology and of plant anatomy can be learned, and the simpler physiological work commonly done in schools can be well carried out on the plants thus available. If the teaching is based on the development, structure, growth and maintenance of the plant as a living being, not only isolated, but as it actually lives in nature, the ecological work proper will bear the right relation to the work necessarily carried on indoors, whichever preponderates in point of time spent on it; and only in this way, the author believes, can plants be used as they should be used in schools, as a means of acquiring a real first-hand knowledge of one of the most important elements of the environment of man.

APPENDIX

Life Forms of Plants.—" Life form " is the name given to the *type* of plant body, with which is associated its life history. Thus the deciduous broad-leaved tree (oak, ash, beech, etc.) is a well-marked life form; the evergreen needle-leaved tree is another; a third is the perennial herb with a persistent underground (or surface) stem (rootstock), the leafy aerial shoots of which arise from fresh buds every spring and die down every autumn; a fourth is the annual herb whose vegetative body dies every season, the plant being continued from year to year solely by means of seed; and so on.

The oldest and most obvious division of the life forms of the higher plants is into trees, shrubs and herbs; but it is clear that each of these must be subdivided, and herbs especially fall into a great number of life-form types. Several detailed classifications of life forms have been proposed, but no one classification is satisfactory from all points of view, because of the great number of combinations of different vegetative characters which actually exist, and the way in which these combinations shade off into one another. The characters which have to be taken into account in classifying life forms are those which are of importance in adjusting the plant to its habitat, for instance the kind of stems produced, of one kind or more than one, annual or perennial, herbaceous or woody; the position of the stems in the habitat, underground, surface or aerial, self-supporting or climbing, or again epiphytic (growing on an aerial part of another plant) or parasitic (getting its food or part of its food from another plant); also the form and nature of the leaves, large or small, broad, narrow, scale-like or absent, evergreen or deciduous, of soft or leathery texture, slightly or strongly protected against evaporation.

It is clear that the possible combinations of such features will be very numerous, though a certain number of well-marked types (such as those mentioned and several others) are constantly repeated in nature and are characteristic of plant communities, occurring in definite habitats. For instance, the

deciduous broad-leaved tree with the leaves relatively slightly protected against evaporation is the characteristic dominant life form of the more favourable soils of Western and Central Europe and of Eastern North America. The shrub or small tree with rather small, leathery, evergreen, strongly protected leaves is characteristic of the Mediterranean region and of other widely separated regions which have the same type of climate in different parts of the world. Large evergreen trees, with large and somewhat leathery, well-protected leaves, are the characteristic dominants of the tropical rain forest. But most communities, all in fact except the very simplest, contain more than one type of life-form. This is partly because different combinations of vegetative characters (i.e. different life forms) will often successfully meet the same set of habitat conditions, and partly because the actual habitats of the different layers or strata of the community are different (see p. 37). Thus plants with small leathery leaves, and plants with reduced scale-like leaves or none at all, may exist side by side; and again, dwarf shrubs with small highly protected leaves, bulbous plants and annuals.

One of the most useful schemes of life forms is that put forward by Professor Raunkiaer of Copenhagen, and is based on the position in regard to the soil surface of the perennating buds, which will continue the growth of the plant. Water plants and marsh plants are considered separately because of their very distinct habitat, which introduces conditions that are not comparable with those of land plants. Succulent plants and epiphytes are also separated in distinct classes. The taller perennials are distinguished as PHANEROPHYTES (broadly trees and shrubs), whose buds are exposed well above the ground-level, and these are classed (necessarily rather arbitrarily) as *Megaphanerophytes* and *Mesophanerophytes* (*MM*.), or trees over 8 metres (say 25 feet in height); *Microphanerophytes* (*M*.), or trees and shrubs of 2–8 m. (6 feet to 25 feet); and *Nanophanerophytes* (*N*.), undershrubs, etc., 10 inches to 6 feet. Then there are *Chamæphytes* (*Ch*.), with buds at the ground-level, or close above (not exceeding 10 inches); *Hemicryptophytes* (*H*.), with buds in the surface layer of soil; and *Geophytes* (*G*.), with buds buried at deeper levels, thus including most of our native and commonly cultivated bulb- and corm-forming plants, as well as the species with deep-lying rhizomes. These may be distinguished as bulb-geophytes, corm-geophytes and rhizome-geophytes respectively. Finally, we have the annuals, or THEROPHYTES (*Th*.).

The proportions of species representing these various classes : life forms in the vegetation of divergent climates is strikingly ifferent. Thus in a moist tropical climate the Phanerophytes ·eatly preponderate over all the other classes put together; in ıe subtropical desert the nanophanerophytes and chamæphytes ɔw shrubs) and therophytes (annuals) are the most numerous species. In North-west Europe, on the other hand, the ›micryptophytes form approximately half of the whole number species. There is also a fair proportion of therophytes owing the prevalence of annual weeds in cultivated land, on road- les, etc. The situation of winter buds in the surface layer of e soil (hemicryptophytes) protects them from moderate frost ıd moderate drought, to which alone the plants of temperate gions are exposed. In the arctic, where the plants are pro- cted during the whole winter by a covering of snow, there is much larger proportion of chamæphytes. The chamæphytes d nanophanerophytes of the subtropical desert have their ıds much more strongly protected against evaporation by ıterproof coverings.

The proportions of the different life forms in various plant mmunities is also characteristic. Forest, the most complex mmunity with the most complex habitat conditions, has prac- ally all the types of land plants (except annuals) represented, ɔugh the hemicryptophytes, in temperate climates, are par- ularly strong. Pasture consists almost exclusively of hemi- ʼptophytes, because buds much above the soil-level would eaten off. Heaths are characterised by the dominance of ɜrgreen chamæphytes and nanophanerophytes, in relation to ld winter climate or snow covering. Communities inhabiting se and soft soils of all kinds are marked by an abundance of nicryptophytes and geophytes with widespreading rhizomes underground runners.

Life form is of course primarily hereditary, though extreme ıditions may force plants normally belonging to one life form ss into the class below by the killing off of the upper buds, instance a micro- into a nanophanerophyte, the latter into hamæphyte, or a chamæphyte into a hemicryptophyte. Life m represents the greatest part of the adjustment of the ɟetative plant body and life history to the habitat conditions, ether this is due to heredity or to the direct effect of the ditions of life.

Methods of Surveying Vegetation.—The graphic methods recording vegetation described in Chapter VIII are those

most generally useful. The most important for detailed study is the large scale quadrat chart in which the position of each individual plant is recorded (standard scale 1 : 10). The "grid-iron" chart (1 : 50 or 1 : 60) is mainly useful for marking the outlines of continuous carpets of more or less uniform vegetation, with or without scattered large individual plants.

At the other extreme from this very detailed work is the recording of larger units on topographic maps (1 : 126,720, 1 : 63,360, 1 : 10,560 and 1 : 2,500 or ½ inch, 1 inch, 6 inches and 25 inches to the mile respectively). Sometimes it is desired to map an area of vegetation—perhaps a quarter or half a mile long—on a larger scale, say 1 : 500, 1 : 1,000, or the like. Such a map has to be made *de novo*, and for this purpose the ordinary "chaining" method used in land survey may be employed. Full details will be found in any textbook of surveying, but a brief outline of methods applicable to vegetation survey may be given here.

First a convenient base line running the length of the area to be mapped must be selected. Every part of this should, if possible, be visible from every other part. The two ends are marked with permanent pegs. It is of the first importance to get the base line *straight*. This is done by planting light wands or rods about 5 feet long at the two ends and then "ranging" these with a series of other rods at intervals of (say) 100 feet till all are seen to be exactly in a line. Standing at one rod and looking towards the other end of the line the next rod should completely hide all the others. A second worker goes to each rod in turn and adjusts its position in accordance with the signals (by hand waving) of the observer. When the line is perfectly straight, it is carefully "chained," i.e. measured with a surveyor's chain or tape,[1] and permanent pegs driven at 100-foot intervals.

The base line having been thus fixed and measured, perpendiculars are erected upon it at suitable intervals, extending to the edges of the area to be mapped. These should be located where they will run *across* the greatest number of physical features (if present) and vegetation boundaries. The right angles can be determined either with the *cross staff* or with the *optical square*.

[1] 100-foot and 50-foot tapes are much more convenient and lighter to carry than chains, but they stretch and shrink, sometimes considerably, if they are wetted. They should therefore be protected from rain as much as possible, and checked against a standard at intervals.

The *cross staff* is planted in the ground on the base line at the point from which a perpendicular is to be run: on its top (at the eye-level) fits a hollow iron prism (cross staff head) of octagonal section, in the side of which are vertical slits. A very narrow slit in one face is diametrically opposite to a broader slit with a vertically running thread in the centre. The head is turned so that on looking through a narrow slit the wire in the opposite slit falls exactly on a vertical rod planted further up the base line. The observer then looks through the narrow slit at right angles to the one falling on the base line, and a rod is stuck in the ground in the direction of the perpendicular, to be erected so that it coincides with the wire in the opposite slit. The line joining the cross staff and the rod which falls on the second wire is perpendicular to the base line.

The *optical square* (which makes a cross staff unnecessary, and is only very slightly more difficult to use) is a hollow cylinder pierced by three openings, two large and rectangular of different sizes and at right angles to one another, and a small circular eyehole diametrically opposite to the smaller rectangular opening. When the instrument is held horizontally, the observer standing on the base line and looking down it through the eyehole, a vertical rod planted on the base line will be seen in the upper part of the field of vision. The lower part of the field is cut off by a block from direct vision, but by means of a mirror at 45 degrees to the line of vision images of objects in a line at right angles to the line of vision are reflected in the lower part of the field. Thus a rod seen in the lower part of the field and falling in a vertical line with the rod on the base line seen in the upper part will be on a perpendicular to the base line drawn from the position of the observer.

The perpendicular, determined either with the cross staff or with the optical square, is then ranged and measured with a chain or tape, and its length recorded. Each perpendicular so made is designated by its distance from the end (origin) of the base line. Secondary perpendiculars (offsets) are then erected on the primary ones in the same way, at suitable intervals, where they will "pick up" (i.e. cross) the largest number of "features" (i.e. physical or vegetational boundaries), and these offsets are noted under the primary perpendiculars to which they belong, each being designated by its distance from the origin of its primary perpendicular.

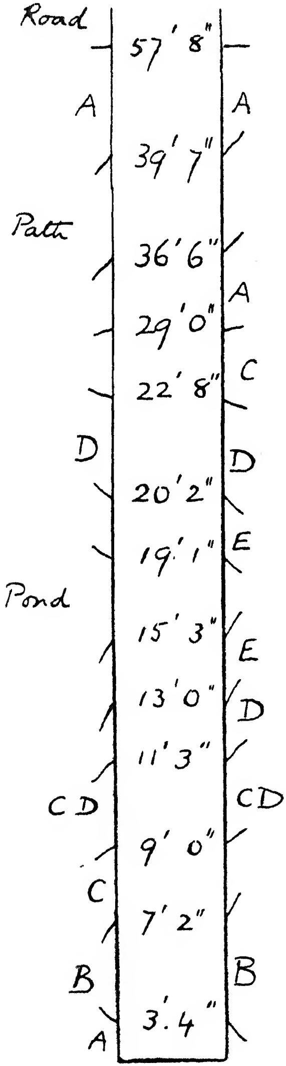
The "features" on the base line are then recorded separately

in a notebook,[1] with the distance of each from the origin of the line on which it occurs (Fig. 14). The data are now complete, and all that remains is to make the map. The base line, perpendiculars, and offsets are drawn to scale on a sheet of paper of the necessary size, the features on each line put in, and then joined up with those on adjacent lines. If the perpendiculars and offsets are sufficiently numerous and have been suitably located, the making of the map will be a straightforward, almost a mechanical job; but should there remain doubt as to certain details, the map may be taken into the field (on a drawing-board) and the boundaries completed by eye on the spot.

When the plant communities to be mapped are well defined and their boundaries not too complicated, the method described above is the best and quickest. But if a great number of communities of complex distribution have to be mapped, the "method of squares" is better. In this, instead of independent perpendiculars and offsets, a complete system of squares covering the area to be mapped is erected on the base line. The side of each square is of any convenient size (say 100 feet, 50 feet or less), and the corners are marked by planting light rods. The right angles are determined as before, but once this has been done and the first squares constructed, any required number of squares can be quickly made by "chaining" the 100-foot intervals along two perpendiculars and "ranging" the remaining corner rods in the two directions, i.e. parallel to and at right angles to the base line. In this method each square is mapped separately on squared paper, and should not be too large to map by eye with reasonable accuracy, and a little assistance in the case of the larger squares from an observer on the side of the square armed with a light 5-foot measuring rod and perhaps an optical square to give the recorder his position in the square. A little practice will soon enable workers to adapt their procedure to the special case.

The methods of survey described above require at least two workers; and a third, to fetch, carry and do odd jobs, is desirable. After the base line has been chosen, ranged and measured, different parties can work at once on different parts of the area, and in this way, after a little experience, and with sufficient

[1] A "surveyor's" or "reporter's" notebook (opening at the end instead of the side) is convenient for this purpose. Two parallel lines, between which the distances are entered, run the length of each page, in the centre, and the data are recorded from the *end* of the notebook, i.e. beginning at the last page and working upwards from the bottom of each page (Fig. 14).



Pep. 148'
Offset. 39'

FIG. 14.—Page of a field survey book, showing data along an offset crossing the side of a small pond. A, B, C, D, E, plant communities, sharply bounded, except C and D, which show a transition zone.

equipment in the way of rods and tapes, a considerable area can be surveyed in the course of an afternoon. It is of course essential that independently working parties should have careful and identical instructions as to the exact method of work, the symbols to be used, and so on, in order that the records may be uniform and sufficiently complete.

The whole of the vegetation should be carefully examined before the survey is started (a previous afternoon should generally be devoted to this), even when the species are known, and a workable scheme of the communities to be recognised decided upon. It is a mistake to erect more perpendiculars and offsets, or squares, than can be comfortably disposed of in the available time. The work should never be hurried at the beginning. Combined quickness and accuracy come with practice. It is rarely advisable (except on private ground) to leave planted rods out overnight, but if the area cannot be completed on one occasion the perpendiculars for the unfinished part of the work can be quickly constructed if permanent pegs (flush or nearly flush with the ground) have been driven at the 100-foot intervals along the base line.

It is rarely worth while to map a very large area in any great detail. The process becomes wearisome and does not repay the time and labour spent upon it. It is much better to spend the time on detailed (quadrat or "gridiron") study of small selected portions, or on a transect across zoned vegetation. To the detailed work a more general map of the whole area may be added if this should seem desirable. For this the 1 : 2,500 Ordnance map may suffice as a basis, or a special survey on the lines described may be carried out. In a senior school class opportunities may thus be found for exercise of the different interests and aptitudes of the members. The survey work is, of course, an excellent exercise in practical geography, and the combination of this with vegetation study may be welcomed by teachers. The whole of the work described, as well as transect and quadrat work, is in the highest degree educational, bringing out and training the powers of observation, accuracy, quickness and ingenuity, as well as bringing the student into the closest touch with nature.

Photography of Vegetation.—It need hardly be said that photographs of plants or of vegetation are of no scientific value unless there is some definite purpose which they fulfil with at least some measure of success. A large proportion of the photographs taken, and even a number of those which get published,

are of little or no value from any point of view, i.e. they are neither instructive nor beautiful. Many subjects are photographed under conditions which offer no prospect of success, and even when the conditions are relatively favourable the plate or film is often carelessly exposed. Students of vegetation who use photography should concentrate on the production of a few really good negatives, each with a carefully considered and definite aim.

There are two main scientific reasons for taking a photograph of vegetation: first the desire to make a picture of a characteristic sample of some definite type, secondly to make a record for the purpose of comparison with other records, for instance with a future photograph of the same spot, or with a quadrat chart.

Under the first head we have the snapshots of the student engaged in reconnaissance or primary survey. Good snaps of characteristic landscapes showing the kind of country and including one or more typical plant communities are interesting and useful, and the more successful negatives may be used to illustrate a published account. It is impossible to lay down hard and fast rules for the taking of these. Landscapes showing good contrast in bright diffused light are likely to be the best subjects. Though some subjects photograph well in bright sunlight, this is generally to be avoided where the vegetation is at all close to the camera, because the excessive contrast and heavy shadows will probably obscure the forms of the plants. When a light stand is carried or the camera can be rested on a support, and the lens focussed, it is of course possible to make a time exposure and to obtain a greater depth of focus by stopping down the lens, including plants in the foreground. Focussing must then be carefully adjusted to get sharp definition of the objects nearest the camera, and the smallest stop used.

Finally, the importance of good composition and contrast may be emphasised. A good pictorial effect is by no means negligible from the scientific standpoint. An effective picture impresses the character of the subject much more strongly than an ugly or poor one.

In the second class of photographs, which are simply scientific records, it is rarely possible to consider pictorial effect, and even a poor negative may be better than none at all, though naturally the best negative possible under the circumstances should be aimed at. In this category come photographs of quadrats, transects or areas which are being mapped. The

quadrat boundary laths, transect tapes, etc., should always be included. They give a certain definiteness to the photograph which is useful and effective.

In photographing a quadrat the camera is best placed a little outside the bottom boundary, tilted forward so as just to include the length of the front lath, focussed on the middle of the quadrat and stopped right down. The quadrat will appear as a trapezium, but the vegetation will be less foreshortened than if the camera is horizontal. When the whole of the vegetation included in the quadrat is very low, forming a carpet with no plants rising much above the general level (e.g. a turf or moss community), it is a good plan also to photograph the quadrat, or part of it, with the camera pointing vertically downwards. This can be managed with the help of a ball and socket "universal joint" screwing to the top of the stand.

Permanent quadrats, especially of communities with well-marked aspects, such as woodland ground vegetation, meadow land, etc., should be photographed in each aspect, i.e. two or three times in the season. At the least all permanent quadrats laid down for the purpose of studying succession must be photographed once a year—if possible when the vegetation is at its maximum luxuriance, and always at the same date, at least within a few days.

Photographic records of vegetation which are intended for comparison with others of the same spot taken at earlier or later periods should be photographed with the camera in *precisely* the same spot at *precisely* the same height and pointing in *precisely* the same direction. Even a slight deviation in any of these respects will render *exact* comparison impossible. The best way to secure this result is to drive a permanent peg into the ground exactly under the middle of the camera, and a taller stake so that it comes exactly in the middle of the picture, and can be focussed upon. If a note is made of the height of the lens above the ground, succeeding photographs which are strictly comparable can then be taken. This precaution is unnecessary when photographing a permanent quadrat with a tilted camera.

Vegetation generally shows up best in a photograph if it is lighted laterally and not from above. For this reason photographs taken shortly after sunrise or shortly before sunset (with the sun behind the camera) are often very satisfactory. The light, of course, must be yellow and not red. A little before sunset, also, the wind often drops and the air becomes calm,

thus enabling a time exposure to be given. Wind is in general a great nuisance to the photographer of vegetation.

Portraits of individual plants should be most carefully focussed. They are often most satisfactory if the plant to be photographed is backed by a piece of material serving as a screen, against which the form of the plant shows up sharply. If taken against a background of vegetation the lines of the portrait are liable to be confused with those of the plants behind which are out of focus.

A good orthochromatic (isochromatic) plate or film should be employed in photographing vegetation. The Wellington "anti-screen" is a suitable brand for ordinary use.

The following paragraphs, kindly contributed by Mr. Hamshaw Thomas, will be useful to those desiring to specialise in the photography of vegetation.

In making exposures it should always be remembered that vegetation usually shows some heavy shadows, and if the details in these are to be visible, sufficient exposure for this purpose must be given. Nothing is more unsatisfactory than photographs with the sharp range of tones giving a "soot and whitewash" effect, and this may be avoided by developing the plates in a solution which contains rather less than the normal amount of alkali. If the negative contains full detail, the desired result may be obtained by printing on bromide paper, by giving a full or abnormally large exposure and by developing with a diluted solution. In order to obtain negatives which are rich in detail pyro-metol is recommended as a developing agent.

Where a long exposure can be given, the Ilford or Wratten pan-chromatic plates may be employed with a light or colour filter (one of the Wratten K series, or the special filter sold by the Ilford Company). In this way a much more correct rendering of the different tones of green occurring in vegetation is obtained. The colour of the filter must not be too deep, or the tones may be "over-corrected," so that the foliage appears abnormally light in the photograph. The plates or films must be developed in the dark (i.e. with the aid of a time-factor), or the plates may be stained before development with a desensitising solution of safranin.

Stereoscopic photography is very valuable for the recognition of individual plants in a community, though the necessity of viewing them through a pair of lenses detracts considerably from their value as a means of illustrating a paper. The appearance of relief seen in stereoscopic photographs is a great help in recognising individual plants which would be scarcely separable

in an ordinary photograph. Stereo-photos are best taken with a stereoscopic camera, but they may also be obtained by making two successive exposures with an ordinary camera which has its optical axis moved by 2–3 inches in a direction at right angles to the plate between the two exposures. By the latter method exaggerated relief may be obtained, or fairly distant objects such as the trees in a wood may be made to show a greater amount of relief than they would possess in photos taken with an ordinary stereoscopic camera, the amount of relief depending on the distance through which the optical axis of the lens is moved.

Determination of Hydrogen-ion Concentration (or "Specific Acidity").—A number of chemical compounds, when dissolved in water, split up into atoms or groups of atoms called *ions*, electrically charged, and these ions are the active agents in chemical reactions. On ionisation of an *acid* compound in water a certain number of the molecules of the acid split up into positively charged *hydrogen ions*, and another constituent depending on the chemical structure of the acid. The free hydrogen ions are the active agents in the chemical effects of acids, so that in the ionisation of a "strong acid" a large number of the molecules are ionised and a correspondingly large number of hydrogen ions set free, while a "weak acid" sets free a smaller number of hydrogen ions. An estimation of the concentration of free hydrogen ions in a solution thus gives a measure of the acid effect of the solution, and it has been found that the results given by such estimations of water-extracts of different soils are often closely correlated with the nature of the vegetation.

There are various ways of measuring the concentration of hydrogen ions in water extract of soil. The electrical method is by far the best, but it is not generally available, and the method of colour indicators gives good results. In this we observe the colour changes produced by the soil extract in certain organic dyes, whose colours have been proved to change in definite ways according to the concentration of free hydrogen ions in a given solution. A selection of these dyes (colour indicators), each of which assumes a certain range of colours through a corresponding range of known hydrogen ion concentration, is used for this purpose. For the most accurate colour determinations it is necessary to use "buffer solutions," i.e. solutions of known ionic concentration whose treatment with a particular indicator gives a series of tints which can be exactly

matched with those obtained by treatment of the soil extract with the same indicator. Such work, however, requires a laboratory and rather too elaborate a technique to be dealt with here.

Results which are sufficiently close to give very useful information as to the range of acidity of a soil habitat can, however, be obtained by the use of a series of six indicators, as explained below. For soils which are neither very acid nor very alkaline two or three indicators only are required.

The hydrogen ion concentration of a solution is ordinarily expressed as the *negative index* (exponent) of 10, the quantity so represented being the actual number of free hydrogen ions in gramme-equivalents per liter. This exponent is known as the " P_H value " (from the " potential," P, of the solution determined by the electrical method).

Thus P_H7 means $10^{-7} = 0 \cdot 0000001$, which is the number in pure water (neutral). P_H6 means $10^{-6} = 0 \cdot 000001$ concentration of hydrogen ions, or 10 times that of pure water, $P_H3 = 0 \cdot 001$, or 10,000 times that of pure water, $P_H1 = \cdot 1$ or 1,000,000 times that of pure water. Thus the lower the index (P_H value) the higher the acidity, each diminution of the index by an integer representing a multiplication of the hydrogen ion concentration by 10. If we call the " specific acidity " of pure water unity, then P_H6 represents a specific acidity of 10, P_H5 a specific acidity of 100, and so on. The use of the set of indicators specified below makes possible the detection of a difference of half an integer ($0 \cdot 5$) in P_H value, and each diminution of this figure represents a multiplication of the specific acidity by $3 \cdot 16$ ($3 \cdot 16 \times 3 \cdot 16 = 9 \cdot 98$, or nearly 10).[1] Thus the results obtained by this method can be expressed as " specific acidities " of 1, 3+, 10, 30+, 100, etc., which is a readily intelligible method of representing the acidities, i.e. the actual concentrations of hydrogen ions.

On the other side of the neutral point, i.e. with P_H values higher than 7, the soil reaction can be expressed as " specific alkalinity " (concentration of hydroxyl or OH ions). Thus $P_H7 \cdot 5$ = sp. alk. 3+, P_H8 = sp. alk. 10, and so on.

The six indicators used are bromphenol blue, bromcresol purple, bromthymol blue, phenol red, methyl red, and cresolphthalein (or phenolphthalein). The first three are used in

[1] Research workers at the subject can detect much smaller differences than this (0.1 of a P_H unit, equivalent to a " specific acidity " factor of 1.26).

PH. Values	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5
			← Acid					Neutral					Alkaline →		
Specific reactions	3000+	1000	300+	100	30+	10	3+	1	3+	10	30+	100	300+	1000	3000+
Bromphenol blue	olive green	brown	blue-purple												
Methyl red	pink			orange	orange-yellow	yellow									
Bromcresol purple	yellow					brown	brown-purple	purple							
Bromthymol blue	yellow						green-yellow	green	blue						
Phenol red	yellow							orange-yellow	orange	orange-red	red				
Cresolphthalein	white										pale pink	pink	red		
Typical soils		← bog-peat →		← upland peat →	← leaf-mold →			← limestone soil →					← "alkali" soil →		

FIG. 15.—Table showing method of determining hydrogen-ion concentration to a difference of PH. 5 with six colour indicators. (After Wherry.)

about 1 per cent. solution in water titrated with dilute sodium hydroxide to their intermediate colours, the phenol red in a 0·5 per cent. solution similarly titrated, the methyl red and phenolphthalein as 0·05 per cent. solutions in 50 per cent. alcohol. A gramme or two of the soil to be tested is placed in an empty tube and 5 cc. to 25 cc. of distilled water added, the tube being well shaken to ensure thorough mixing. The solid matter may then be compacted with a glass rod and the tube supported at an angle of 45 degrees until the bulk of the suspended matter has settled. The more or less clear liquid is then decanted or pipetted off into another tube and a drop or two of one of the indicators added. Unless the soil is believed to be decidedly acid or alkaline, one of the central indicators, e.g. bromthymol blue, should be first used. If a green colour is given, the soil is neutral, and this may be confirmed by the purple colour of bromcresol purple being unchanged, and by phenol red giving an orange yellow colour. If on the other hand the bromthymol blue gives a yellow colour, the soil is acid, and the degree of acidity may be determined by using successively bromcresol purple, methyl red, and bromphenol blue, or as many of these as may be necessary. The table (Fig. 15) will show clearly how the different specific acidities may be determined.

If the water remains turbid for long after compacting the soil, more of the indicator must be used to give a clear result, and the more turbid the water the less certain the result. Soils containing particles finer than those of sand (see p. 155) give an extract which remains more or less turbid for some hours.

It may be noted that the great majority of soils in this country range between $P_H 5$ and $P_H 7$, i.e. from moderately acid to neutral.

This method is recommended by its author (Dr. Wherry) for "field use," but in this country, where distances are not great, it is much more convenient to bring the soil samples home in small tins and carry out the tests at leisure, so that the finer particles may have time to settle before adding the indicator.

The indicators can be obtained from the principal British firms of manufacturing chemists. A complete set of the six indicators, packed for field use, is prepared by the La Motte Chemical Products Company, 13, W. Saratoga Street, Baltimore, Md., U.S.A.

DETERMINATION OF CARBONATES, OF MAGNESIA, LIME AND POTASH, AND OF "SALT" (CHLORIDES) IN SOILS

By H. J. PAGE

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Preparation of Sample.

The soil to be examined should be spread out in the laboratory to dry, and then pounded up with a wooden pestle and passed through a 3 mm. sieve, the stones retained on the sieve being rejected. The sifted soil should be stored in a dry bottle and clearly labelled with full particulars.

Total Carbonates.

A rough idea of the amount of carbonates in the soil may be readily obtained as follows: Moisten a few grammes of the soil in a beaker with just sufficient water to cover it; stir to remove air bubbles, and then add about 10 cc. of strong hydrochloric acid, stir round, and observe the result carefully. If there is a marked effervescence of gas with frothing, the soil contains at least 1 per cent. of carbonates; a slight but perceptible effervescence indicates the presence of roughly ½ to 1 per cent. of carbonates. If there is no visible result, but a faint crackling can be heard, the soil contains less than ½ per cent. carbonates, while the absence of even this latter indication suggests that the soil is devoid of carbonates and probably acid.

The total carbonates of the soil can be most conveniently determined by the use of Collin's Calcimeter.[1] Failing this, a fair idea of the amount may be obtained in apparatus which can be fitted up in the laboratory, in which the volume of carbon dioxide liberated when a known weight of the soil is treated with hydrochloric acid is measured.

[1] This apparatus can be obtained, with instructions for its use, from Messrs. Brady and Martin, Newcastle-on-Tyne.

SOIL ACIDITY.

If the soil is found to be devoid of carbonates, it can be readily tested for acidity by Comber's test, which is carried out as follows: 2 or 3 grammes of soil (which need not be air dried) are shaken vigorously in a test tube with a 5 per cent. solution of potassium salicylate and then allowed to stand; when the soil has settled the supernatant liquor is red in colour if the soil is acid; otherwise the colour is only brownish yellow.

MAGNESIA, LIME AND POTASH.

Preparation of Extract.—20 grammes of the powdered soil are placed in a flask of resistant glass, covered with about 70 cc. of strong hydrochloric acid, and boiled for a short time over a naked flame. The flask is then loosely stoppered and the contents digested on the water bath for forty-eight hours; the solution is then cooled, diluted and filtered, and the residue on the filter paper well washed. The combined filtrate and washings are made up to 250 cc.

Magnesia and Lime.—A suitable aliquot of the above solution (say 50 cc.) is evaporated to dryness in a porcelain basin; the residue is then gently ignited and at the same time ground up with a glass pestle until it is converted into a dry red powder. It is then moistened with strong hydrochloric acid, allowed to stand for five minutes, diluted with water and filtered; the whole of the residue is carefully washed on to the filter paper and the washing continued until the liquid which runs through is no longer acid. To the filtrate is added a little ammonium chloride solution, followed by ammonium hydroxide until the liquid is slightly alkaline. The precipitate consists of the hydroxides and phosphates of iron and aluminium; the liquid is filtered and the residue carefully washed (if desired, this residue can be ignited and weighed, giving the amount of Fe_2O_3, Al_2O_3, P_2O_5, corresponding to that weight of the soil which the aliquot represents). To the filtrate add 25 cc. of boiling oxalic acid solution containing a little hydrochloric acid. Add a few drops of methyl orange and then ammonia in small quantities at a time, with constant stirring until the liquid is yellow, then add 25 cc. of hot ammonium oxalate solution, and after standing for four hours filter and wash with hot 1 per cent. ammonium oxalate until a few drops of the filtrate, after acidifying with nitric acid, gives no precipitate with silver nitrate.

Reserve this filtrate for the determination of magnesia (see below), wash the filter paper and residue twice with a small quantity of hot water, and then transfer the residue from the filter paper to a beaker by means of a stream of water from the wash-bottle. The part remaining on the filter is removed by allowing warm dilute sulphuric acid to pass through it several times, the liquid being collected in the same beaker into which the residue was washed. To the turbid solution in the beaker 20 cc. of sulphuric acid (1 : 1) are added, and after dilution with hot water to about 300 cc. the liberated oxalic acid is titrated with decinormal potassium permanganate, 1 cc. $\frac{N}{10}$ $KMnO_4 = 0 \cdot 002005$ gm. Ca.

The filtrate reserved for magnesium estimation is made just acid with hydrochloric acid, heated to boiling, and 25 cc. of sodium phosphate solution added. A volume of 10 per cent. ammonia, roughly equal to one-third of that of the solution, is added, the solution allowed to cool, and after standing for a few hours the precipitate is filtered off on a filter paper or through a Gooch crucible, washed with 2·5 per cent. ammonia, dried and ignited, at first very slowly, the temperature being later increased until the precipitate is pure white; cool in a desiccator and weigh as $Mg_2P_2O_7$, $\frac{2Mg}{Mg_2P_2O_7} = 0 \cdot 2184$.

Potash.—Take a further aliquot of the original extract and, if the original soil did not effervesce with acid, add to it ½ gramme of pure $CaCO_3$; in any case add 10 cc. of 5 per cent. baryta solution, then evaporate to dryness and ignite with grinding as above. Boil the residue with distilled water, filter and wash. To the filtrate add 2·5 cc. of pure perchloric acid (sp. gr. 1·12) and concentrate in a glass basin on the sand bath until dense white fumes are given off, cool and add with stirring 20 cc. of 95 per cent. alcohol. Decant the clear liquid through a tared filter paper or Gooch crucible, and add to the precipitate 40 cc. of 95 per cent. alcohol, previously saturated with potassium perchlorate, then transfer the precipitate to the paper or crucible and wash with a further 50 to 100 cc. of the same alcohol until the runnings are no longer acid (special care must be taken, when a filter paper is used, to remove the last traces of acid from the paper, otherwise the latter will char during drying). Dry at 100° and weigh as $KClO_4$, $\frac{K}{KClO_4} = 0 \cdot 2822$.

"Salt" (Sodium Chloride and Other Chlorides).

100 grammes of finely powdered soil are shaken vigorously (preferably in a mechanical shaker) for five minutes with 500 cc. of distilled water; 2 grammes of powdered alum are then added and the whole stirred up and allowed to settle. 20 cc. portions of the clear liquid are pipetted into stoppered bottles and a known volume of decinormal silver nitrate added to each, sufficient being taken to throw out the whole of the chloride.[1] 10 cc. of 95 per cent. alcohol are added, and the liquid shaken until the silver chloride is coagulated and the liquid is clear; 2 cc. of 4 per cent. ferric sulphate solution and 5 cc. of dilute nitric acid are added, and the excess of silver nitrate estimated by titration with decinormal ammonium thiocyanate until the liquid is just pink. From the volume of silver nitrate required to precipitate the chloride the amount of this in the soil, expressed as sodium chloride, can be calculated in the usual manner.

Total Soluble Material.

If it is required to estimate the total soluble material in the soil, the latter should be treated in the same way as before, but instead of adding alum the clear extract must be obtained by filtration through a Pasteur-Chamberland filter. A known volume of this extract is then evaporated to dryness on the water bath in a weighed porcelain basin and weighed. This gives the total soluble material, while by igniting at a dull red heat until the whole of the organic matter is burned off, and reweighing, the amount of soluble inorganic material may be determined.

[1] A soil recently flooded with sea-water might give an extract of which 20 cc. would require at least 3 cc. of decinormal silver nitrate for the complete precipitation of the chloride. A larger amount of silver nitrate solution would be needed for a salty soil in which considerable evaporation had occurred after flooding with sea-water.

CLASSIFIED LIST OF BOOKS AND PAPERS

(1) For School Use

(a) Suitable for Direct Use in Schools

1. PRAEGER, R. LLOYD, Weeds: Simple Lessons for Children. (Cambridge University Press, 1913. Price 2s. 6d.)
2. RUSSELL, E. J., Lessons on Soil. (Camb. Univ. Press. Price 3s.)
3. GREGSON, M. M., The Story of our Trees. (Camb. Univ. Press, 1912. Price 3s. 6d.)

(b) Reference Works for Use by the Teacher and Older Pupils

4. JONES, W. NEILSON and RAYNER, M. C., A Text-Book of Plant Biology. (Methuen, 1920. Price 7s.)
5. RUSSELL, E. J., Soil Conditions and Plant Growth. (Fourth edition. Longmans, 1921. Price 16s.)
6. EVANS, E. PRICE, Local Ecology as a Basis for School Botany. (*School Science Review*, June, 1920.)

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7. HOOKER, J. D., A Student's Flora of the British Islands. (Third edition. Macmillan, 1884. Price 10s. 6d.)
8. Illustrations of the British Flora. (Reeve. Price 12s. 6d.)
9. DRUCE, G. C., A Botanist's Pocket Book. (Bell. Price 5s.)

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20. TANSLEY, A. G., and ADAMSON, R. S., Reconnaissance in the Cotteswolds and the Forest of Dean. (*Journ. Ecol.*, 1. 1913.)
21. MOSS, C. E., Geographical Distribution of Vegetation in Somerset: Bath and Bridgwater District. (With coloured vegetation map. Royal Geogr. Soc., 1906.)

Ireland.

22. PETHYBRIDGE, G. E., and PRAEGER, R. LLOYD, The Vegetation of the District lying South of Dublin. (With coloured vegetation map. *Proc. Roy. Irish Acad.*, 25B. 1905.)

(*b*) *Monographs and More Detailed Studies.*

Scotland.

23. CRAMPTON, C. B., and MACGREGOR, M., The Plant Ecology of Ben Armine, Sutherlandshire. (With coloured vegetation map. *Scot. Geogr. Mag.*, 29. 1913.)
24. MATTHEWS, J. R., The White Moss Loch, a Study in Biotic Succession. (*New Phytologist*, 13. 1914.)
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51. YAPP, R. H., and COLLABORATORS, The Salt Marshes of the Dovey Estuary. (*Journ. Ecol.*, 4. 1916, and 5. 1917.)
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